Attentional processes in mosquito-eating jumping spiders: search images and cross-modality priming

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Contents

Statement

There are a number of published papers throughout my thesis, both thesis chapters and appendices (the latter for background reading). I verify that, in all these published papers, I had a central role. I contributed substantially to all parts of the work, with this including being involved in designing the experiments and, with the help of research assistants, in carrying out of the experiments. I had a primary role in writing up each of these papers. I also analysed all of the data and prepared nearly all of the figures and tables.

Abstract

Evarcha culicivora, a species of jumping spider (Araneae: Salticidae) from the Lake Victoria region of East Africa, has unusual prey-choice behaviour. It preferred prey is blood-carrying mosquitoes. It also has unusually complex mate-choice behaviour, with mutual mate choice being pronounced. This thesis is a study of *E. culicivora*'s prey-choice behaviour and mate-choice behaviour, as well as a study of processes underlying selective attention in this unusual species. *E. culicivora* uses olfaction in unique and often surprising ways. This includes identifying potential mates by odour alone, as well as choosing the odour of potential mates that have recently fed on blood-carrying mosquitoes. The odour of potential mates also primes both sexes for escalating conflict with potential rivals, as well as priming selective attention to the masked odour of specifically potential mates. Besides all this, the odour of blood-carrying mosquitoes primes *E. culicivora* to selectively attend to the masked odour of specifically this prey. Moreover, the appearance of blood-carrying mosquitoes and of potential mates primes *E. culicivora* to selectively attend to specifically the appearance of cryptic blood-carrying mosquitoes and cryptic potential mates, respectively. Vision and olfaction can even work together, with olfactory and visual cues from blood-carrying mosquitoes priming *E. culicivora* to selectively attend to the appearance and odour, respectively, of blood-carrying mosquitoes. Furthermore, *E. culicivora* has a poorly-understood relationship with two plant species, *Lantana camara* and *Ricinus communis*, and *E. culicivora* can identify these two plant species by odour alone. These plants may be relevant to this salticid as a nectar source by which it supplements its insect diet, but these plants may also be as sites at which *E. culicivora* males and females find potential mates, with *E. culicivora*'s interactions on these plants being especially exaggerated and complex.

Chapter 1

Introduction

This thesis is a study of processes underlying selective attention in *Evarcha culicivora*, a jumping spider (Araneae, Salticidae) from East Africa. Just how this came about is a story in itself. In fact, it is a story filled with mystery and intrigue, where both the beginning and ending is unconventional to say the least. For telling this story to its full effect, an unconventional writing style is required for both the beginning and the ending of this thesis.

"Don't Cross me – I study spiders!" (the words of an exasperated spider researcher)

Never in a million years did I think I would study spiders for my PhD. Elephants maybe, or horses almost definitely, but spiders? They used to terrify me! When I was five years old, my teacher held up a picture of a katipo and warned us not to go near one because we might get bitten. I hadn't thought of spiders being able to bite people before, and the very thought scared me so much. From then on, in my mind's eye, whenever I saw a spider, it had a red stripe on its abdomen and was going to hurt me, and so I always screamed and ran away when I saw one. Many of my garden adventures as a little kid in Tauranga (New Zealand), looking for insects, were ruined by the mere presence of spiders. Eventually, though, by the time I was about 10 years old, I put two and two together – I'd never been bitten by a spider, and I am much

bigger than they are. If I can leave them alone, then surely they can leave me alone? I tried it, and that worked for a while. But then I realised that I couldn't leave them alone.

I came to study spiders the hard way. Not only did I have to deal with a fear of them at an early age, but I also thought, later on, that they were boring. I started off at Canterbury hoping to study both psychology and zoology, but those plans appeared to go down the drain when I nearly failed my zoology courses in my first year and I decided I would never study zoology again. I continued with psychology, which I found very interesting, but watched my friends continuing on in zoology and appearing to enjoy themselves. I caught one of them reading an article on jumping spiders one day and asked him why he was doing that. When he replied that jumping spiders are interesting, I very firmly said "No, they're not!" After all, how much can a jumping spider do? These are small animals, meaning they've got small brains. How could they possibly do anything that is very interesting?

Well, would you believe it, but someone in Zoology (as it used to be then) allowed me to skip the prerequisites to his 3rd year Animal Behaviour course. It was the one course that I had hoped all along I could do, and so having the opportunity to take it was a dream come true. The amazing thing about this course was how it opened my eyes to the things animals can do, even the animals that I thought were boring. Pretty soon, I was learning about a species of jumping spider, *Portia fimbriata*, that could pluck the silk of another spider's web to trick it into thinking that a prey item had fallen into its web, so that it would move closer to where *Portia* was waiting, and closer to the jaws of death (Jackson & Wilcox, 1998). To my amazement, *Portia* could also take detours to reach a prey item, even if it couldn't even see that prey item for part of the way (Tarsitano & Jackson, 1994, 1997). There

was clearly something ticking inside these animals. Needless to say, when I went home to Tauranga that summer, I was busy out in the garden looking for other members of *Portia*'s family.

Strange as it may seem, when I met my own study spiders in the lab for the first time it was actually a pretty underwhelming experience. The spiders I'm referring to are *Evarcha culicivora*, a species of jumping spider from the Lake Victoria region of East Africa. Sounds impressive, but these spiders are small, and they don't look up to much. The males and females are variable in size, but on average they are only about 5 mm in body length (Cross et al., 2007a). Nor is their colour very exciting. If I could imagine a jumping spider from the tropics, I would picture something of dazzling iridescent colour that sparkled like a jewel, not the little brown spiders I saw in front of me. The males have little red faces and little tufts of white hair around their faces, but that was completely unnoticeable to me on the first meeting. You must forgive me for judging a spider by its cover, but I was soon to realise that, with these spiders, there was much more to learn than meets the eye.

"Who can fathom the mind of a spider?" (Keith C. McKeown, 1952)

I felt drawn to study *Evarcha culicivora* after hearing that this little animal preys by preference on blood-carrying mosquitoes. This may simply sound disgusting to a person living in New Zealand, a country where mosquito-borne diseases such as malaria are non-existent. To some, Africa and its troubles may seem like a world away. In my family, however, conversations about Africa and malaria were commonplace. My mother had lived in Zambia for the first eight years of her life, and

when she was two years old she nearly died of cerebral malaria. Obviously, she survived, and after an adult dosage of quinine she got better again. However, I grew up fully aware of how serious malaria is. It's a killer. *Anopheles gambiae*, the world's most efficient vector of human malaria, is often referred to as the most dangerous insect on Earth (Miller & Greenwood, 2002), and for good reason. Every year something like 400 million people fall ill with malaria, and 1–3 million of these people die, mainly children aged under 5 years, and mainly in Africa (Marshall, 2000). A number of large-scale measures have been taken to reduce the impact of malaria, including subsidising availability of pesticide-treated mosquito nets (e.g. Vogel, 2002), development of antimalarial drugs in a race to keep ahead of *Plasmodium*'s ability to evolve resistance (e.g. Miller & Greenwood, 2002), attempting to develop a malaria vaccine (Taubes, 2000), and even attempts to engineer a malaria-resistant mosquito to replace natural populations (Enserink, 2000).

The wonderful thing about *E. culicivora* is that it lives in the very part of the world where malaria is especially serious. Whoever would have thought that these small, brown spiders could be targeting something so deadly? It's always the ones you least suspect. In fact, *E. culicivora* likes mosquitoes so much that we typically refer to them as 'Mosquito Terminators' (MT for short). It's much easier to look past *E. culicivora*'s miniscule appearance when you know what they can do.

The thing about jumping spiders is that they can see remarkably well for animals of their size. A very good reason why these spiders aren't boring is that being able to see well enables them to perform complex tasks. Most spiders have poorly developed eyesight, but jumping spiders have acuity that surpasses animals of their size, and rivalling that of "conventional" animals used in behaviour research (Harland & Jackson, 2000, 2004). Jumping spiders have eight eyes, six of which (the

'secondary eyes') are positioned around the side of the carapace and function primarily as motion detectors (Land, 1969a, 1969b, 1971). It is the forward-facing 'principal eyes' that process details about objects being viewed.

With its principal eyes, *E. culicivora* can accurately discern the difference between different prey items. In its natural habitat there is an abundance of mosquito-sized insects from the families Chaoboridae and Chironomidae known locally as 'lake flies' (Okedi, 1992). They look like mosquitoes, but they are really non-biting midges that form in huge swarms (numbering in the millions) over Lake Victoria, raining down on the shoreline vegetation and human dwellings and forming a blanket of seething insect life. Within this teeming mass, mosquitoes are only the minority, but *E. culicivora* is actually remarkably good at picking out a mosquito from a crowd. Certain features of the mosquito, such as its abdomen colour and shape, may be helping *E. culicivora* to discern a mosquito from other insects in the vicinity (Jackson et al., 2005).

However, you're in trouble if you even do so much as let *E. culicivora* smell a blood-carrying mosquito. These spiders go nuts at the smell of blood. One whiff of the stuff, and *E. culicivora* is practically given a licence to seek and destroy, launching into feeding frenzies where as many as 20 mosquitoes can be killed in one sitting, even if the spider doesn't intend to eat all of them. Or even worse, male *E. culicivora* may launch into courtship display, as if smelling the blood turns him on for seeing a potential mate. It's the stuff nightmares are made of.

Something that is fascinating, and slightly repulsive, about *E. culicivora* is that diet and attraction to the opposite sex appear to be tightly linked. Spiders that have recently eaten a blood-carrying mosquito apparently smell more attractive to potential mates than spiders that have eaten something else, such as a lake fly, or even a

mosquito that hasn't fed on blood (Cross et al., unpubl.). Body size also plays an important role in mate attraction, with larger mates being more attractive than smaller ones (Cross et al., 2007a). Again, diet may be playing a part because having blood in the diet when young may result in a larger adult body size.

One thing I hadn't taken on board when I initially heard about *E. culicivora* was just how complicated its mate-choice behaviour really is. I guess I was so absorbed in its bizarre prey-choice behaviour that I hadn't thought this animal could be complicated in any other way. Turns out I was wrong again. When I first started out working with *E. culicivora*, one of my jobs was to sit and watch males and females interact. I thought that it couldn't possibly be difficult. It was. Because jumping spiders are such visual animals, their courtship repertoires tend to involve a lot of movement to attract, and sustain, the attention of a potential mate (Jackson & Pollard, 1997). Jumping spiders, in fact, have some of the most complex courtship displays known to the animal kingdom. However, of all the jumping spiders studied to date, *E. culicivora*'s courtship repertoire is apparently the most complex (Cross et al., 2008)! It seemed pretty typical for me to land such a complicated job, but all the hours spent watching them helped me to appreciate what this small animal is capable of doing.

One of the most surprising things I noticed was the tendency for males to eat females, rather than the other way round (Cross et al., 2008). Whenever I sat down to watch an interaction, I was armed with a little paint brush so that I could interrupt any interactions that were about to go wrong. It could get a bit nerve-wracking at times because I couldn't afford to lose study animals as the result of an interaction gone wrong. What often seemed to happen was that the male would display to the female for a while, but if the female kept moving away the male would sometimes creep up

on her and eat her! About half of the human population enjoys hearing this story; the other half is not amused.

The other bizarre thread to *E. culicivora*'s mate choice behaviour is that this spider actually shows an association with two plant species that grow wild in the same habitat, *Lantana camara* (family Verbenaceae) and *Ricinus communis* (family Euphorbiaceae). *L. camara* is a weed (native to tropical and subtropical America; Ghisalberti, 2000), while *R. communis* is native to tropical Africa (Cronk & Fuller, 1995). One thing we already knew about jumping spiders is that they feed on nectar (Jackson et al. 2001) and pollen, and so *E. culicivora*'s association with these plants, especially *R. communis*, is not surprising in this context. *R. communis* has extra-floral nectaries, containing mainly fructose, glucose and sucrose, in about equal amounts, and also at least 14 different amino acids (Baker et al., 1978). In other words, this source of sugar may be useful to *E. culicivora* for supplementing its insect diet.

However, there's more to *E. culicivora*'s association with plants than this. To my amazement, these spiders went crazy when they could smell certain plant odours, especially from *L. camara*. It actually reminded me very much of the effect that catnip has on cats, the way that a plant can produce a drug-like effect in an animal. When I presented *E. culicivora* males with *L. camara* odour, they'd sometimes launch into courtship displays as if they could see a female in front of them. The interesting thing was that more often than not, there was no female present, just a male inside an empty apparatus with air pumping through. It got pretty disturbing whenever the males turned around and started courting me. I didn't think I looked anything like a female *E. culicivora*.

Later on, I also found out that my spiders respond strongly to different draglines. Draglines are the lines of silk that spiders deposit when they move about

their environment. Not only do draglines assist spiders as they move about (they provide some sort of anchor in case the spider falls, for instance), but they also carry pheromonal information about that spider, such as whether it's male or female, and what species it is (this being an example of what biologists refer to as a 'signpost signal') (Pollard et al., 1987). Again, the males went crazy when they were presented with draglines from a conspecific female. I'd heard that some species of jumping spider respond to the draglines from a potential mate in this way (Pollard et al., 1987), but the behaviour I was seeing from *E. culicivora* seemed extreme even in this context.

"Who can fathom the mind of a spider researcher?" (Anonymous)

I'd made this discovery about *E. culicivora* and draglines while I was visiting *E. culicivora*'s homeland. I was in Kenya from July 2006 until January 2007, mainly staying at Thomas Odhiambo Campus in a little remote village, Mbita Point, on the shores of Lake Victoria in western Kenya. It was my first proper trip out of New Zealand (my first trip was to Australia when I was only eight, which doesn't really count), and so it's safe to assume that a lot of things there were very different for me. I suddenly had to eat food I'd never eaten before, or even heard of, like tilapia, ugali and sukuma wiki. Of course, one immediate lifestyle change I had to make was to avoid getting malaria. Over there, almost all the locals have had malaria, and I was always hearing about people I knew being sick with malaria, but it was OK for me because I could afford to take antimalarial drugs (Lariam – my friend!). It did seem a bit strange at first having to sleep under a bed net and burn mosquito coils, as well as

use insect repellent, but I quickly got used to the routine. Another thing I had to get used to was the fact that I really was living in *E. culicivora*'s homeland. If I saw *E. culicivora* running along the lounge wall, it was OK. I wasn't in a quarantine lab where any spiders running free had to be put back in their cages. There really was something special about being in *E. culicivora*'s home country.

Africa! The land of elephants, zebras, giraffes, lions and flamingos. And spiders! I saw all of these, all in their homeland and mostly in the wild (the elephants I saw were kept at an orphanage). It was such an amazing experience to go and Kenya is a beautiful country. And yet there is another side to Africa, where many of the people are living in poverty and battling disease. I could see it as we went on car trips. The "roads" over there are very bad, and so it takes a long time to get anywhere. When I first went to Mbita Point, we went by car, which took about eight hours from Nairobi, but even getting to the supermarket in Kisumu would take three. We had to time car trips carefully as well because we needed to get back by nightfall, especially if we knew it might rain at the end of the day (no one wants to get stuck in mud!). This often meant we had to get up very early and I recall having to get up at 4 in the morning one time just to go to the supermarket! Anyway, one of the striking things about going on these trips was going through the villages along the way. There were always people just sitting outside their "houses" waving to us as we went by. Or they would try to sell us things like newspapers, pineapples, roasted maize, puppies and rabbits. The thing that struck me was just how hard life is for these people. It's no fun trying to make a living if you and other members of your family are often faced with disease. And it's not exactly easy living on less than $1 a day.

In Kenya, many of the locals are wary of a number of animals, including spiders. They'd probably see *E. culicivora* as something to squash, rather than being a

little cat-like friend. But being in Kenya helped me to see even more clearly what a helpful little animal *E. culicivora* is. The thing with malaria is that there is not one single thing that will eliminate it. There are just lots of pieces to the puzzle that have to be fitted together. *E. culicivora* is just one little piece, but my feeling on it is that even a very little piece deserves to be investigated further.

Crossing into cross-modality priming

The beauty of working with *E. culicivora* is how it's given me the chance to explore my interests in animal cognition. Coming from a background in psychology, I have been interested in cognition for a long time and wanted to learn more about what makes animals tick. When I was six years old, I decided that a machine should be invented that could tell me what animals are thinking. Well, we're still no further on in that respect, but there is a lot we can learn from experimentation.

I can talk about animal cognition now, but there used to be a time when this topic was unheard of. The very idea of 'spider cognition' would have been thrown out the window! Fortunately for me, animal cognition has slowly gained scientific respectability over the years (Kamil, 1998; Shettleworth, 2001; Wasserman & Zentall, 2006; Yoerg, 1991), even though it was a neglected topic in both psychology and biology for a long time. Two traditions dominated the study of animal behaviour in the 20th century, ethology and comparative psychology. Ethology placed more emphasis on ultimate causation (Morgan, 1896), while comparative psychology placed more emphasis on proximate causation (Watson, 1919), and early on both of these traditions more or less explicitly excluded cognition from their theoretical

frameworks (Boakes, 1984; Richards, 1987; Mazur, 1998). However, the study of animal cognition seems to build a bridge between the two, giving us a perspective that had been missing (Kamil & Bond, 2006; Shettleworth, 1998, 2001).

Perhaps, though, I'm getting a little ahead of myself. Back in the early days there actually was someone, an ecologist, who did seem to appreciate the role of cognition in animal behaviour (foraging behaviour, to be precise; see Cross & Jackson, 2006). His name was Lukas Tinbergen, and he did some remarkable field-based research in the Netherlands on insectivorous birds beginning in 1946 but ending abruptly in 1955 with his untimely death at the age of 39 (Baerends & de Ruiter, 1960). His work was published posthumously five years later (Tinbergen, 1960) where his hypothesis on search images was presented. Tinbergen envisaged search images as perceptual changes, the idea being that the predator, after discovering a particular type of prey, "gets an eye for" or "learns to see" this particular type of prey. By "learning to see", it is clear that previous experience by the predator with a particular type of prey primes the predator to be selectively attentive to specific features of this particular prey (see Blough, 1989, 1991, 1992; Brodbeck, 1997; Dawkins 1971a, 1971b; Langley, 1996; Langley et al., 1996; Reid & Shettleworth, 1992). In experiments, an important way of demonstrating selective attention in this context is by using cryptic prey (i.e., when previously-encountered prey are difficult to find, the predator needs to use selective attention to find them again in the future).

Tinbergen (1960) also suggested that predators "perform a highly selective sieving operation on the visual stimuli reaching their retina" (p. 332). 'Sieving', or 'filtering', implies that certain features of the prey are ignored, whereas other, more salient features are attended to. It may also imply that the predator ignores other distractors in the environment, such as features of non-prey. Research on humans has

shown evidence of sieving through visual-search paradigms, where a particular target with a certain configuration of features is searched for within a crowd of distractors lacking in this configuration (Pashler, 1998; Treisman, 1986; Treisman & Gelade, 1980).

It really is uncanny reading Tinbergen's paper nearly 50 years later. Here is someone who understood something about cognition, but was trying to explain it to a group of people who didn't, or perhaps refused to, understand. I can't imagine how difficult it would have been for someone in that position, and yet there is so much that we have learned about animal cognition since then. It truly is an understatement to say that Tinbergen was ahead of his time!

Spiders are not "conventional" subjects for the study of search images but they may be surprisingly useful. Because jumping spiders can see so well, they can potentially make the fine-grained discriminations necessary for forming a search image. Actually, this was recently shown (Jackson & Li, 2004) in *Portia labiata*, a jumping spider from the Philippines which specialises in eating other spiders. *P. labiata* could visually discriminate between two different species of spider and form a search image for the spider it had recently encountered (Jackson & Li, 2004).

Although search-image research, and priming research in general, usually focuses on one sensory modality (usually vision), recent cognitive research has highlighted that a cue in one modality (e.g., olfaction) may cause attentional changes in another modality (e.g., vision). This is known as cross-modality priming. For example, cross-modality priming might occur when detecting a particular odour cue from a particular prey item prepares an animal for detecting a particular visual cue from the same prey item. In recent years, cross-modality priming has become an important area of research in human cognitive psychology (for example, see Calvert

et al., 2004; Driver & Spence, 1999; Pauli et al., 1999; Spence & Driver, 2004; Stein et al., 2001), and there have also been studies showing that cross-modality priming is relevant to understanding the behaviour of non-human animals (for example, see Candolin, 2003; Partan & Marler, 1999; Shine & Mason, 2001). Cross-modality effects have been shown experimentally in the predatory behaviour of jumping spiders (Clark et al., 2000; Jackson et al., 2002), confirming that these spiders have brains with the computational ability required for cross-modality priming.

As I mentioned earlier, one way this applies to predators is that they may become selectively attentive to the appearance of a prey item after being exposed to the prey's odour (i.e., a specific odour, not appearance, might trigger selective attention to specific features of appearance). Another way of putting this might be that the odour of a particular prey type could call up a pre-formed search image (i.e., a disposition for selective visual attention to features of this prey type's appearance). This was something I wanted to investigate more fully, partly because I always wanted to be known for doing something related to my surname. In all seriousness, however, search images aren't generally considered in the context of two different sensory modalities working together (as mentioned earlier, they are usually only considered in the context of visual attention being primed after an animal sees something) and yet, if you think about it, a lot of animals may be using cues from more than one sensory modality when they are forming search images. For example, if an animal forms a search image after eating a prey item, it may be that chemical information as well as visual information about that prey is priming selective attention. This is something that perhaps a lot of researchers don't fully appreciate (for an elegant exception, see Bond & Kamil, 2002), but I became increasingly interested in examining this in more detail.

However, my idea behind studying search images also had a twist. It seemed that search images were only considered in the context of foraging, but I felt that search-image formation could be relevant in other contexts as well. In particular, *E. culicivora* seemed good at finding mates while on *L. camara*. When looking at this plant, you'd think it would be hard for a small animal like *E. culicivora* to find anything in that jungle of leaves and flowers. However, it seemed that search images were at play. In particular, the odour of *L. camara* may actually be priming *E. culicivora* to find potential mates. Whoever would have thought, after all those hours of watching (and laughing at) *E. culicivora* males displaying in the olfactometer in the presence of *L. camara* odour, that they might actually be teaching me something interesting about selective attention and search images? I really should have learned by then not to be surprised. But I was.

Searching for hidden treasure

It was especially interesting to consider how *E. culicivora* might use olfaction when forming search images. 'Olfactory search images' are similar to the more conventional search images (i.e., visual search images), except that here, after encountering an odour from a particular type of prey, a predator becomes selectively attentive to the odour from that prey. Over the years, however, there has been very little research in this area, even in work with much bigger animals, and I actually found myself becoming increasingly unhappy even with the little research that had been done. Forget about doing something related to my surname – here was something that made me live up to my surname! Feeling particularly cross, I thought

that the literature on olfactory search images was missing something important. Olfactory search images really should be envisaged as being about selective attention, just like with visual search images.

As far as I'm aware, only three papers have been published on olfactory search images (Gazit et al., 2005; Nams, 1991, 1997) and, in one of these papers (Nams, 1991), the author blatantly states that 'crypticity' is a term that applies more to vision than to the other senses. It's like this author just threw his arms up in the air, as if he didn't really care about the relevance of selective attention in the search-image concept and how it might be possible to make odour cryptic in his experiments. This sort of attitude never fails to surprise me. We are talking about research that, done in the right way, could potentially be very interesting, but I couldn't shake off the feeling that there was a huge chasm in the research that no one was prepared to fill. My feeling on it, however, was that it may be more challenging to demonstrate selective attention in the context of olfaction, but that does not, in any way, mean it is impossible.

Whenever I think of olfactory search images, there's always one thing that comes to mind and that is a sniffer dog at an airport that is trained to find the odour of a particular drug. The sniffer dog has to search for this particular odour among many other odour sources that may be present in the luggage but, once it detects the correct odour, it responds by barking. It always amazes me when I think of how sensitive the dog's sense of smell is and how it can accurately perform this kind of task. Yet, the more I thought about it, the more I could imagine other situations where animals might need to make use of olfactory search images. For example, animals that are especially reliant on olfaction may encounter many odour sources on a daily basis. This made me start to imagine the different situations in which an animal might need

to encounter particular odour sources hidden (or 'masked') by other odour sources. If you look at it that way, an odour source might be considered 'cryptic' and the animal would need to use selective attention to find it.

In the previous work on olfactory search images, Nams (1991, 1997) showed that skunks could detect a particular food odour from greater distances over time. More recently, Gazit et al. (2005) found that sniffer dogs trained to find explosives identified more jars containing TNT when their recent exposure to TNT was high, but found fewer jars when their recent exposure was low. Although I was excited when I found out that olfactory search images had been considered with sniffer dogs, and I also thought it was plausible that skunks could form olfactory search images, I couldn't help but feel a bit frustrated with this research. I really got the impression that these authors hadn't fully appreciated the relevance of selective attention when the skunks and dogs use search images for finding particular odour sources. For one thing, these authors hadn't considered the possibility of using masked odour in their experiments.

Yet here I was doing research with a little animal that I knew was really good at using olfaction, both in the context of finding its preferred prey, blood-carrying mosquitoes (Jackson et al., 2005), and in the context of finding potential mates (Cross & Jackson, in press). I started to imagine *E. culicivora* on an aromatic plant like *L. camara*, and it made me wonder about the possible relevance of olfactory search images. For instance, perhaps *E. culicivora* needs the help of olfactory search images when trying to find a potential mate on this plant. More precisely, perhaps *E. culicivora* would need to use selective attention to find the odour of a potential mate if this odour is masked by the odour from the plant. I felt that, at the very least, this deserved to be investigated further. However, throughout this time, there was another

question I pondered over. Was it really possible that a little jumping spider could actually showcase to the world the first solid evidence of olfactory search images?

Developing the spider story

Let's get back to the basics, however. Before I could do any work on topics relating to selective attention, such as olfactory search images and cross-modality priming, I needed to learn more about the stimuli that are salient to *E. culicivora*. This was my rationale for the work in Chapters 2–6.

Chapter 2 is an experimental study of whether *E. culicivora* can identify potential mates on the basis of odour cues alone. Until now, there had been many studies with other salticid species that respond to contact chemical cues in silk (e.g., Clark & Jackson, 1995; Jackson, 1987; Pollard et al., 1987; Taylor, 1998; also see references in Huber, 2005), but studies on odour-based discrimination in these animals had been lacking. This presented me with the exciting opportunity of considering this, for the first time with salticids, using *E. culicivora*. From previous research (Cross et al., 2007a, 2008), I knew that both sexes of *E. culicivora* are active in courtship and in making mate-choice decisions, and I hypothesised that both sexes of *E. culicivora* can also identify potential mates through odour-based cues alone. Chapter 2 has been accepted for publication in *Behavioural Processes*.

Chapter 3 is an extension of the work in Chapter 2, but in ways that might chill you to the core. This time, I examined whether both sexes of *E. culicivora* choose mates on the basis of odour cues alone and whether *E. culicivora*'s unusual prey preferences and mate choice behaviour might be tightly linked. In particular, I

asked the bizarre question of whether feeding on blood makes individuals of *E. culicivora* more attractive to the opposite sex. My hypothesis was that, by feeding on blood-carrying mosquitoes, *E. culicivora* acquires a blood odour that it uses as perfume to attract potential mates. The very thought is enough to keep you awake at night.

In Chapter 4, I now consider whether *E. culicivora* can identify the draglines of potential mates. Although this has been considered before in research on many other salticid species (see Huber, 2005; Pollard et al., 1987), this had not been investigated in *E. culicivora* until now, and my hypothesis was that both sexes of *E. culicivora* can discriminate the draglines of opposite-sex conspecifics (i.e., potential mates) from the draglines of opposite-sex heterospecifics (i.e., unrelated salticids of the opposite sex). However, in this chapter I also make a start at considering something more novel – whether *E. culicivora* is a salticid that can determine the quality of a potential mate on the basis of silk cues alone. In particular, results from previous research (Cross et al., 2007a) indicated that both sexes of *E. culicivora* choose mates by size alone. In Chapter 4, I extend this previous work by testing two hypotheses: 1) that both sexes of *E. culicivora* can determine size by silk cues alone and 2) both sexes of *E. culicivora*, when using silk cues alone, can identify its preferred mates. Although I see the results from this work as preliminary, I also see a promising area here for future research.

For something even more novel, Chapter 5 now shifts to the question of whether plants play an important role in the mate-choice behaviour of *E. culicivora*. In this chapter, I provide a descriptive summary of how individuals of *E. culicivora* behave when they are on *Lantana camara* and *Ricinus communis*. As part of my MSc, I provided a detailed description of the behaviour patterns used by *E. culicivora*

during intraspecific interactions (see Cross et al., 2008), but these interactions were all staged in empty cages. How individuals interact when they are on plants instead of in empty cages is considered for the first time here in my PhD thesis. Although *E. culicivora*'s behaviour during interactions is known to be particularly complex (Cross et al., 2008), it is even more so when individuals meet on plants. Making these observations was important because it provides a foundation for research on how individuals of *E. culicivora* might use selective attention while they are on these plants. The summary I include in this chapter was published within a much larger article (Cross et al., 2008) in *New Zealand Journal of Zoology*.

Chapter 6 is an extension of the work in Chapter 5, but now I consider whether the odour of *L. camara* and the odour of *R. communis* are salient to *E. culicivora*. The observations I made of *E. culicivora* individuals on these plants in Chapter 5 suggested that *L. camara* and *R. communis* are an important part of *E. culicivora*'s biology. Moreover, I knew from previous work (Cross & Jackson, in press; see Chapters 2 and 3; Jackson et al., 2005) that *E. culicivora* makes pronounced use of olfaction, and my hypothesis for Chapter 6 was specifically that individuals of *E. culicivora* can identify *L. camara* and *R. communis* on the basis of odour cues alone. There are only a few examples known of salticids associating with particular plants (e.g., see Romero, 2004; Romero & Vasconcellos-Neto, 2005), and the work in this chapter is an important starting point for investigating how strongly individuals of *E. culicivora* might associate with *L. camara* and *R. communis*. The work in this chapter is also important for being a first step toward more thoroughly investigating whether the odour of these plants might be relevant to *E. culicivora* in selective-attention tasks. This work has been published in *New Zealand Journal of Zoology*.

From Chapter 7 onwards, I consider topics more directly relevant to my primary research interest – selective attention. However, I will warn you now that Chapter 7 is bizarre! In this chapter, I investigate the stimuli that trigger courtship display in males of *E. culicivora*, my hypothesis being that *E. culicivora* males perform courtship displays when they are presented with stimuli that are linked with finding potential mates. I consider questions such as 1) can the odour of a conspecific female trigger courtship display? 2) How about the odour of *Lantana camara*? 3) How about a blood-carrying mosquito? 4) How about blood alone? Although the results in this chapter are somewhat shocking, maybe even spine tingling, they also highlight the kinds of stimuli that may be particularly important for *E. culicivora* during tasks relating to selective attention and, in particular, when *E. culicivora* is searching for a potential mate.

Chapter 8 now turns to the role of cross-modality priming in the context of intraspecific conflict. An especially convenient thing about jumping spiders is that, because they are such visual animals, they will respond to their reflections in mirrors as if they are seeing potential rivals. Using mirrors in this way helps to eliminate potential confounding variables that might arise in experiments when two living spiders interact with each other. In this chapter, I consider whether males and females of *E. culicivora* show higher levels of aggression to potential rivals (i.e., their reflections in a mirror) when the odour of opposite-sex conspecifics, rather than the odour of opposite-sex heterospecifics, is present.

Earlier work (Cross et al., 2007b) had shown that males of other salticid species (*Portia africana* and *Jacksonoides queenslandicus*) can make this discrimination and show more aggression to a rival when the odour of a potential mate is present, but this had not been investigated with *E. culicivora* until now. An

important part of the work in Chapter 8 was comparing the results I got with *E. culicivora* with the results for *P. africana* and *J. queenslandicus*, as well as for another species, *Portia fimbriata*. Unlike *E. culicivora*, where both the male and female have a strong role in courtship and in choosing mates, the behaviour of the other three species is more typical of salticids in general (i.e., the male is more active in courtship and the female is more choosy; see Jackson & Pollard, 1997). I considered whether these different mating strategies might influence how males and females respond to their mirror images, with my hypothesis being that, in mating strategies where both sexes are active in courtship, both the male and the female will show more aggression to a potential rival when they are presented with the odour from a potential mate.

In Chapter 8 I also extend the work of Chapter 2 by considering how males and females of *E. culicivora* respond to their mirror image when presented with the odour of opposite-sex conspecifics instead of the odour of same-sex conspecifics. My hypothesis was that *E. culicivora* can discriminate the odour of opposite-sex conspecifics from the odour of same-sex conspecifics by odour cues alone, and I predicted that both sexes of *E. culicivora* would show more aggression to their mirror image when presented with the odour of opposite-sex conspecifics. The work in Chapter 8 has been published in *Behavioural Processes*.

In Chapter 9, however, I really start to get to the crème de la crème of selective-attention research with *E. culicivora*! Here, I also consider cross-modality priming, but now in the context of whether the odour of blood-carrying mosquitoes primes *E. culicivora* to find specifically blood-carrying mosquitoes by sight. However, I also consider if cross-modality priming can also work in the other direction by investigating whether seeing blood-carrying mosquitoes primes *E.*

culicivora to find the odour of specifically blood-carrying mosquitoes. My hypothesis is that *E. culicivora* uses cross-modality priming in both directions for finding its preferred prey. However, in this research, the prey *E. culicivora* had to find were either cryptic or conspicuous. This suggests that search images are at play if *E. culicivora* is primed to find a cryptic mosquito. The work in this chapter is important because I consider the hypothesis that a cue in one sensory modality triggers a search image in another sensory modality, something that isn't normally considered in search-image research, let alone in work with spiders! The work in Chapter 9 had been accepted for publication in *Journal of Experimental Biology*.

Chapter 10 is an extension of Chapters 8 and 9. Here, I investigate whether individuals of *E. culicivora*, as well as individuals of another salticid species, *P. fimbriata*, show more aggression to a potential rival (again, an image in a mirror) in the presence of odour from preferred prey rather than odour from non-preferred prey. My hypothesis was that individuals of *E. culicivora* and of *P. fimbriata* show more aggression in the presence of odour from preferred prey. Although the results in this chapter were somewhat surprising (I can't tell you the results now – that would give it away!), they provide important insights into the value of preferred prey for these two salticid species.

In Chapter 11 I go back to the topic of search images and investigate whether *E. culicivora* forms vision-based search images (i.e., 'conventional' search images). However, the work in this chapter is unconventional because I consider whether *E. culicivora* forms search images in more than one context (for finding blood-carrying mosquitoes and for finding potential mates). Previous work has suggested that visual cues from blood-carrying mosquitoes and from potential mates are especially salient to *E. culicivora* (Cross et al., 2007a; Jackson et al., 2005), and my hypothesis is that

E. culicivora forms search images in each of these two different contexts (i.e., after seeing blood-carrying mosquitoes, *E. culicivora* uses selective attention to find blood-carrying mosquitoes but not potential mates, and after seeing potential mates *E. culicivora* uses selective attention to find potential mates but not blood-carrying mosquitoes).

In Chapter 12, my penultimate chapter, I extend the work of Chapter 11 by considering whether *E. culicivora* can form olfactory search images for blood-carrying mosquitoes and for potential mates. Again, previous work has suggested that olfactory cues from blood-carrying mosquitoes and from potential mates are especially salient to *E. culicivora* (Cross & Jackson, in press; see Chapter 2; Jackson et al., 2005), and again my hypothesis is that *E. culicivora* forms search images in each of these two different contexts but this time it is *olfactory* search images that I consider. This chapter also finally gave me the chance to explore whether there are ways for making odour cryptic.

Chapter 13 is where I look back and reflect on my work, discussing how my findings may have some importance within the field of animal cognition. I consider the human, as well as the animal, literature on selective attention, and I make some suggestions for future research in this chapter.

After the Acknowledgements, I have, as Appendices, six published papers. I was a co-author on each of these and I include them for background information. They may also help in clarifying the rationale and concepts behind some of the work in the main part of my thesis. I will insert these papers in chronological order.

Cross, F. R., & Jackson, R. R. (2006). From eight-legged automatons to thinking spiders. In K. Fujita & S. Itakura (Eds.), *Diversity of Cognition* (pp. 188–215). Kyoto: Kyoto University Press. This was a fun book chapter I worked on in the

first year of my PhD, and it was my first publication! In this chapter, we review literature on topics relating to selective attention, such as search images and cross-modality priming. Writing this book chapter was important to me personally because it helped me to develop research ideas for my PhD, and it was especially relevant as the driving force behind my interest in research on olfactory search images.

Jackson, R. R., Walker, M. W., Pollard, S. D., & Cross, F. R. (2006). Influence of seeing a female on the male-male interactions of a jumping spider, *Hypoblemum albovittatum*. *Journal of Ethology, 24*, 231–238. This is the first paper in a series on male-male conflict. Here we investigated whether males of *Hypoblemum albovittatum*, a New Zealand species of jumping spider, escalated conflict in the presence of different stimuli (potential mates, prey, etc).

Cross, F. R., Jackson, R. R., Pollard, S. D., & Walker, M. W. (2006). Influence of optical cues from conspecific females on escalation decisions during male-male interactions of jumping spiders. *Behavioural Processes, 73*, 136–141. In the next paper in the series, we investigate whether seeing a conspecific female rather than a heterospecific female primes males of seven salticid species (*Bavia aericeps*, *Euryattus* sp., *Hypoblemum albovittatum*, *Jacksonoides queenslandicus*, *Marpissa marina*, *Portia africana* and *Simaetha paetula*) to escalate conflict with other conspecific males.

Cross, F. R., Jackson, R. R., Pollard, S. D., & Walker, M. W. (2007). Cross-modality effects during male-male interactions of jumping spiders. *Behavioural Processes, 75*, 290–296. In the third paper in the series, we extend the work of the previous paper by investigating whether males of these seven salticid species escalate conflict with other males (in this case, their reflections in a mirror) when presented with the odour of conspecific females instead of heterospecific females. The work in

this paper was especially important for developing the research on *E. culicivora* in Chapters 8 and 10.

Cross, F. R., Jackson, R. R., & Pollard, S. D. (2007). Male and female mate-choice decisions by *Evarcha culicivora*, an East African jumping spider. *Ethology, 113*, 901–908. In this paper, we present findings that are especially important as background for some of the work in my PhD thesis. We show that both sexes of *E. culicivora* choose mates by vision alone. Before mating, both males and females prefer larger potential mates. After mating, although males still prefer larger females, females switch preferences and choose smaller males. We discuss how these decisions might relate to how cannibalism is expressed in *E. culicivora*. Males of *E. culicivora* are more cannibalistic than females, with larger males being especially dangerous. We propose that females are especially reluctant to take the risk of choosing a larger, more dangerous, male after they have mated. Males, on the other hand, appear to be less worried by the prospects of becoming a female's dinner. Part of the work for this paper was carried out for my MSc. This paper was fun and it sparked some media interest, both nationally and internationally.

Cross, F. R., Jackson, R. R., & Pollard, S. D. (2008). Complex display behaviour of *Evarcha culicivora*, an East African mosquito-eating jumping spider. *New Zealand Journal of Zoology, 35*, 151–187. In this mammoth paper, we describe the different behaviour patterns used by males and females of *E. culicivora* during intraspecific interactions, and we describe how these behaviour patterns are combined into sequences. A large portion of the material in this paper was work that I carried out during my MSc. However, the paper also includes new work in which I considered how *E. culicivora* individuals interact when they meet on plants (covered in Chapter 5 of this thesis). Having this paper in an appendix might also be useful for

some general background information, including anatomical details and behaviour definitions, as well as details on rearing methods. However, I don't expect anyone to sit down and read this long paper from beginning to end. Think of it more as a general-reference guide.

The chapters in my thesis are written as stand-alone manuscripts and this means you may notice some necessary repetition throughout my thesis. Something else to warn you about is that formatting will vary between chapters. This is because different chapters have been prepared for different journals and I have retained the formatting specific to each journal.

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Chapter 2

Mate-odour identification by both sexes of *Evarcha culicivora*, an East African jumping spider

In this chapter, I investigate the role of olfaction for *Evarcha culicivora* in the context of identifying potential mates. Many previous studies have explored whether salticids identify potential mates through chemical cues on silk (e.g., Huber, 2005; Pollard et al., 1987), but *E. culicivora* is a salticid that uses olfaction for identifying its preferred prey, blood-carrying mosquitoes (Jackson et al., 2005) and, in this chapter, I show that both sexes of *E. culicivora* also use olfaction for identifying potential mates. This has not been documented for any salticid species until now.

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Mate-odour identification by both sexes of *Evarcha culicivora*, an East African jumping spider

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Abstract

Evarcha culicivora is an unusual salticid spider because each sex actively courts the other and both sexes make distinctive mate-choice decisions. Here we use olfactometer experiments for investigating the ability of each sex to identify potential mates on the basis of odour alone. Test spiders spent more time in the vicinity of opposite-sex conspecific source spiders, regardless of whether or not these source spiders had previously mated, when the alternatives were conspecific individuals of the same sex, juveniles or a control (no odour source). This trend held regardless of the test spider's and source spider's age after reaching maturity and, for male test spiders, it held regardless of the test spider's mating status. However, after females had mated they no longer expressed a preference for male odour.

Chapter 3

Blood as perfume and the mate-choice decisions of a mosquito-eating jumping spider

In Chapter 2, I showed that both sexes of *Evarcha culicivora* identify potential mates on the basis of odour alone. In Chapter 3, however, I extend this work by exploring whether *E. culicivora* can also make mate-choice decisions by odour alone. *E. culicivora* is a species with pronounced mutual-mate-choice behaviour (Cross et al., 2007, 2008; see Appendices 5 and 6) and is also a species with unusual prey-choice behaviour, having a preference for blood-carrying mosquitoes (Jackson et al., 2005). Here, I consider whether its unusual prey-choice behaviour and mate-choice behaviour are tightly linked.

Sunset over Lake Victoria as seen from Mbita Point, Kenya

Blood as perfume and the mate-choice decisions of a mosquito-eating jumping spider

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Abstract

Evarcha culicivora (Araneae, Salticidae) feeds indirectly on vertebrate blood by choosing as preferred prey blood-carrying female mosquitoes. Mutual mate-choice behavior is also pronounced in this species. Here we show that, when *E. culicivora* feeds indirectly on blood, it acquires a diet-related odor that makes it more attractive to the opposite sex. The mate-choice decisions of adults of both sexes were investigated in a series of experiments based on comparing how long the test spider remained close to the odor of one source spider on one day and to the odor of a different source spider on the following day. Four different maintenance diets for source spiders were used in these experiments: blood-fed female mosquitoes (Culicidae, *Anopheles gambiae ss*), sugar-fed *A. gambiae* females, *A. gambiae* males, lake flies (Chironomidae, *Nilodorum brevibucca*). Both sexes of *E. culicivora* spent more time close to the odor of opposite-sex conspecifics that had been on a diet of blood-fed mosquitoes (blood diet) instead of any of the three non-blood diets. Opposite-sex conspecifics that had been on a non-blood diet became more attractive once they were switched to a blood diet. That the attractive odor from blood dissipates was shown when spiders became less attractive once they were switched to a non-blood diet or subjected to a fast. However, there was no evident preference for the odor of a same-sex conspecific on a blood diet instead of a lake-fly diet. These findings are discussed in the context of sexual selection and sensory exploitation.

Key words: mosquitoes, olfaction, predation, Salticidae, sensory exploitation, sexual selection

Introduction

Chemoreception, including olfaction, widely acknowledged as the most ancient sensory modality (1, 2), is used by animals in many different contexts (3). For example, chemoreception might play a particularly important role in the context of reproduction when an animal needs to distinguish mates from rivals and conspecific individuals from heterospecific individuals (3), as well as determine relatedness (4) and the health of a potential mate (5). Here we consider how diet-derived odor might influence the mate-choice decisions of *Evarcha culicivora*, a jumping spider (Araneae: Salticidae) known for having unusual prey-choice behavior and for being a species in which mutual mate choice is pronounced (6). Although all spiders probably rely to some substantial extent on chemoreception (7), salticids are better known for having unique, complex eyes (8) and vision based on a level of spatial acuity that is unrivalled by animals of comparable size (9). Yet salticids use tactile, auditory and percussion signals, either in conjunction with or as alternatives to vision-based signals (10, 11). Salticids are also one of the spider families for which we have the most experimental evidence of reliance on chemical signals (12, 13).

E. culicivora is an unusual salticid species because it feeds indirectly on vertebrate blood by actively preferring blood-carrying mosquitoes as prey (14, 15). However, the dominant mosquito-size dipterans in *E. culicivora*'s habitat are non-biting midges (known locally as 'lake flies') from the families Chaoboridae and Chironomidae (16), and *E. culicivora* can readily discriminate between the lake fly and the mosquito by sight and by olfaction (14).

Evarcha culicivora also identifies opposite-sex conspecific individuals (i.e., potential mates) not only by sight but also by odor (6, 17). Here we consider whether there is a link between this predator's unusual diet and its mate-choice decisions, our

hypothesis being that, by feeding on blood-carrying mosquitoes, *E. culicivora* acquires an odor that is preferred by potential mates. Our findings come from using an olfactometer designed for 'retention testing' (17), each individual test spider being presented with odor from one source spider on one day and odor from a different source spider on the following day (odor presented on first day determined at random). The rationale for this test design was an expectation that the spider would stay near a more preferred odor longer than near a less preferred odor.

Results

How the source spider's maintenance diet influences retention time

As predicted by our hypothesis, retention times for test spiders were significantly longer when the opposite-sex source spider had been maintained on a blood diet instead of a non-blood diet (Table 3.1). This trend held regardless of whether source spiders had or had not already mated (mated compared with virgin source spiders; male test spiders: $Z = 0.993$, $P = 0.321$; female test spiders: $Z = 1.399$, $P = 0.162$).

Diet did not appear to influence retention time when same-sex source spiders were used (Table 3.1), and scores using opposite-sex source spiders were significantly higher than scores using same-sex source spiders on the same diets (male test spiders: $Z = 3.816$, $P < 0.001$; female test spiders: $Z = 6.136$, $P < 0.001$).

How switching to a blood diet influences retention time

For males, retention times were significantly longer when the source spiders were females that had been switched from a lake-fly diet to a blood diet 1 day earlier, instead of remaining on a lake fly diet. Retention times were significantly longer also when the female source spiders had been switched to a blood diet 14 days previously instead of 1

day previously, and significantly longer when the female source spiders had been switched to a blood diet 28 days previously instead of 14 days previously (Table 3.2).

For females, retention times were significantly longer when the male source spiders had been switched to a blood diet 14 days previously instead of 1 day previously (Table 3.2). However, retention times were not significantly longer when the male source spiders had been switched to a blood diet 1 day earlier, instead of remaining on a lake-fly diet, and not significantly longer when the male source spiders had been switched to a blood diet 28 days previously instead of 14 days previously.

On the whole, these findings appear to show that, even in the short term, a blood diet makes the odor of opposite-sex conspecifics more attractive, and attractiveness seems to increase when the duration of blood feeding increases. Although two of the comparisons that were significant for males were not significant for females, scores for females were not significantly different from scores for males, regardless of whether the opposite-sex source spiders had been on a blood diet for 1 day instead remaining on a lake-fly diet ($Z = 1.512$, $P = 0.131$), had been on a blood diet for 14 days instead of for only 1 day ($Z = 1.165$, $P = 0.244$), or had been on a blood diet for 28 days instead of for 14 days ($Z = 0.762$, $P = 0.446$).

How switching to a lake-fly diet and fasting influence retention time

Retention times for male and female test spiders were significantly shorter when source spiders were opposite-sex individuals that had been switched from a blood diet to a lake-fly diet 1 day earlier, instead of remaining on a blood diet. Retention times were also significantly shorter when opposite-sex source spiders had been switched from a blood diet to a lake-fly diet 14 days earlier instead of only 1 day earlier (Table 3.3).

Moreover, retention times were significantly shorter when the source spiders were opposite-sex individuals that, after being maintained on a blood diet, were subjected to a 7-day fast instead of not fasting and were also significantly shorter when opposite-sex source spiders had fasted for 14 days instead of for 7 days (Table 3.4).

Discussion

Our experimental findings show that feeding on blood-carrying mosquitoes makes the odor of *E. culicivora* males and females more attractive to the opposite sex, with even a single blood meal sufficing to make either sex more attractive to the other and with attractiveness tending to increase when the time on a blood diet increased. Continued access to blood meals appears to be important, as the attractiveness opposite-sex source spiders gained from a blood diet was lost when access to this diet was brought to an end either by a switch to a non-blood diet or by a fast.

This is the first evidence that *E. culicivora*'s unusual prey-choice behaviour might be linked to this species' mating strategy, but it may be common for animal courtship routines to be based in part on the use of odors that have salience in another context. Examples include pheromones of noctuid moths mimicking the plant volatiles used by females for locating oviposition sites (18). Male fruit flies attract potential mates by using ginger root oil as a perfume (19). Some bird species incorporate aromatic plant material in their nests, with this possibly functioning as protection against parasites as well as functioning as a method of attracting potential mates (20, 21). There is also evidence from studies on salamanders and voles that odor derived from high-quality diets makes individuals more attractive to the opposite sex (5, 22).

The highly specific prey-choice behavior by which *E. culicivora* appears to

specialize on a difficult-to-satisfy diet suggests that good-genes hypotheses (23) might be useful for explaining why this species bases mate-choice decisions on diet-related odor, and an important next step will be to determine whether there is heritable variation in the spider's ability to acquire the diet-related attractive odor. However, another perspective on sexual selection, sensory exploitation (24), may be especially relevant for understanding *E. culicivora*'s odor-based mate-choice decisions. Sensory-exploitation hypotheses have been proposed in other research on salticid courtship behavior (10, 25). For example, males may sometimes attract the female's attention during courtship by using specific movement patterns that simulate the movement-related cues by which females normally detect prey. However, a closer parallel to how *E. culicivora* uses diet-derived odor may be found in how male euglossine bees store odor-generating compounds from orchid flowers in special sacs on their hind leg tibia and use this odor to attract females (26), but with some important differences. The bees do not rely on orchid odor for finding food, but *E. culicivora* uses blood odor in the context of feeding as well as in the context of courtship. For the euglossines, it is only the male that collects odor-generating compounds (27), whereas both sexes of *E. culicivora* acquire odor from mosquitoes. For euglossine males, there is a problem of acquired odor attracting the unwanted attention of other males (28), but there is no evidence that, for *E. culicivora*, acquired odor is attractive to same-sex conspecific individuals.

The role of sensory exploitation in *E. culicivora*'s biology appears to be less than straightforward, as the odor derived from preying on blood-carrying mosquitoes does not seem to attract the opposite sex simply by exploiting a predisposition to respond to this odor as a prey-identification cue. We found evidence of acquired odor making individuals more attractive only when the source spider was an opposite-sex

conspecific individual. This suggests that the attractant is an odor derived by some additional processing after ingestion or perhaps a prerequisite for the acquired odor to render an individual more attractive to the opposite sex is for this odor to be paired with another odor that identifies the individual's sex.

Materials and Methods

General

Standard procedures were used for rearing and maintenance (for details, see 29). All individuals used as test and source spiders (see below) were from the F2 or F3 laboratory generations (cultures derived from individuals collected at our field site: Mbita Point, western Kenya). Once juveniles dispersed from their egg sacs, they were kept isolated from encounters with other conspecific individuals until used in an experiment. Source spiders were fed three times a week, and were assigned at random to one of four maintenance diets (14). There was a 'blood diet' (prey always mosquitoes that had fed on human blood 4–5 h before used as prey for the spider) and there were three 'non-blood diets', namely spiders fed only on lake flies, only on male mosquitoes or only on female mosquitoes that were sustained on sugar alone (no blood meals). Test spiders were fed three times a week and were maintained on a diet of blood and of lake flies. All mosquitoes were *Anopheles gambiae ss* from culture. All lake flies were *Nilodorum brevibucca* (Chironomidae), collected locally as needed. Test spiders and, if not fasted, source spiders were always used in experiments on the next day after feeding.

For spiders, the terms 'male' and 'female' always refer to adult males and adult females (both sexes 5 mm in body length). Virgin: no contact with conspecific individuals after emerging from egg sac (reached maturity 14 days before tested).

Mated: like virgin, except mated on the 7th day after reaching maturity and then tested 7 days later. Mated females had not oviposited.

Experimental methods

During testing, air was pushed successively through a stimulus chamber, a holding chamber and an exit chamber (Fig. 3.1). Airflow was always adjusted to 1500 ml/min (Matheson FM-1000 airflow regulator) and there was no evidence that this airflow setting impaired locomotion or had any adverse effects on *E. culicivora*'s behavior. The stimulus chamber was a glass cube (inner dimensions, 70 × 70 × 70 mm) made from 5–mm thick glass and each cube had two holes (diameter 20 mm, centered on opposite sides of the cube, each hole plugged with a rubber stopper). Source spiders were put in the stimulus chamber 30 min before testing began.

The holding chamber was a glass tube (length 90 mm, inner diameter 15 mm, rubber stopper in one end, other end open). The open end of the holding chamber fit securely in the hole in the exit chamber, flush with the inner wall of the exit chamber. At the other end of the holding chamber there was a hole in the stopper with a glass tube going through to the stimulus chamber. A nylon-netting screen over the stopper (new netting for each test) ensured that the test spider could not enter the stimulus chamber, with the only way out of the holding chamber being via the opening into the exit chamber. The exit chamber was another glass cube identical to the stimulus chamber.

The test spider was first kept in the holding chamber for 2 min, with the holding chamber not yet connected to stimulus and exit chambers. The end of the holding chamber that would go into the exit chamber was plugged with a rubber stopper. For starting a test, this stopper was removed and the holding chamber was positioned

between the stimulus and exit chamber, but with a prerequisite that the test spider had to be in the half of the holding chamber distal to the exit chamber. If this prerequisite was not met at the end of the 2-min pre-test period, starting was delayed until the spider moved on its own accord into the distal half of the chamber and remained there for 2 min. Testing was aborted if this criterion was still not met after waiting 15 min, but aborted tests were rare (< 5% for any given experiment).

All tests began between 0800 and 1400 hours (laboratory photoperiod 12L:12D, lights on at 0700 hours) and lasted for a maximum of 60 min. Once testing began, we recorded the test spider's latency to leave the holding chamber (i.e., time elapsing between test beginning and spider entering exit chamber; maximum time allowed, 60 min). By default, the spider's latency to leave was recorded as 60 min whenever the 60-min test period ended with the test spider still in the holding chamber. No individual was used in more than one pair of retention tests and no individual was used more than once as a source spider. Between tests, the olfactometer was dismantled and cleaned with 80% ethanol, followed by distilled water, and then dried. For access to the interior when cleaning, there was a removable top on each stimulus and exit chamber.

Data analysis

As our data often failed to meet the assumptions required for parametric analyses, we used Wilcoxon tests for paired comparisons (null hypothesis: latency when tested with source spider 1 matched latency when tested with source spider 2). A score was calculated for each test spider by subtracting latency when tested with source spider 2 from latency when tested with spider 1 (positive score: spider spent more time in the holding chamber when tested with spider 1; negative score: spider spent more time in

the holding chamber when tested with spider 2). Using Mann-Whitney *U*-tests, we also compared the scores for different groups of test spiders (null hypothesis that scores for one group matched scores for another group). Wilcoxon test results are in Tables 3.1–3.4, whereas Mann-Whitney test results are in text (for details about statistical procedures, see 30).

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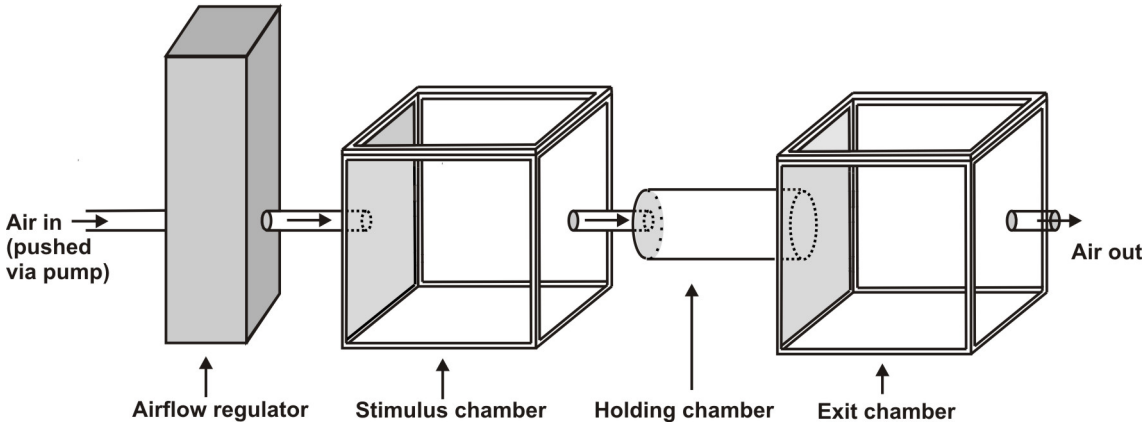

Fig. 3.1. Olfactometer for retention testing (not drawn to scale). Arrows indicate direction of airflow. Testing started with test spider in holding chamber at end distal to exit chamber. Test spider has access to exit chamber during test. Test spider's view of odor source obstructed by black paper taped to outside of stimulus-chamber wall that faced holding chamber.

Table 3.1. Scores for *Evarcha culicivora* when tested for discrimination of diet-related odor. Source spiders maintained on a variety of diets. Unless stated otherwise, all test and source spiders virgins. For each row, $n = 50$. Score: time spent near source spider 2 minus time spent near source spider 1

Test spider	Source spider 1	Source spider 2	Median score	First quartile	Third quartile	Wilcoxon test
Male	Female on blood diet	Female on male-mosquito diet	14.5	6.0	22.0	$Z = 4.870$, $P < 0.001$
Female	Male on blood diet	Male on male-mosquito diet	25.5	13.0	32.0	$Z = 5.691$, $P < 0.001$
Male	Female on blood diet	Female on sugar-fed female-mosquito diet	9.0	-2.0	20.0	$Z = 3.398$, $P < 0.001$
Female	Male on blood diet	Male on sugar-fed female-mosquito diet	20.0	9.0	37.0	$Z = 5.426$, $P < 0.001$
Male	Female on blood diet	Female on lake-fly diet	18.5	-1.0	27.0	$Z = 4.810$, $P < 0.001$
Female	Male on blood diet	Male on lake-fly diet	19.0	9.0	31.0	$Z = 5.476$, $P < 0.001$
Male	Mated female on blood diet	Mated female on lake-fly diet	11.5	-1.0	24.0	$Z = 3.929$, $P < 0.001$
Female	Mated male on blood diet	Mated male on lake-fly diet	13.0	-1.0	31.0	$Z = 3.577$, $P < 0.001$
Male	Male on blood diet	Male on lake-fly diet	-0.50	-6.0	3.0	$Z = 1.394$, $P = 0.163$
Female	Female on blood diet	Female on lake-fly diet	0.0	-4.0	3.0	$Z = 0.643$, $P = 0.511$

Table 3.2. Scores for *Evarcha culicivora* when tested for effect of switching source-spider diet from lake flies to blood. All test and source spiders virgins. For each row, $n = 50$. Score: time spent near source spider 2 minus time spent near source spider 1

Test spider	Source spider 1	Source spider 2	Median score	First quartile	Third quartile	Wilcoxon test
Male	Female on blood diet for 1 day	Female on lake-fly diet	7.0	-1.0	21.0	$Z = 3.228$, $P = 0.001$
Female	Male on blood diet for 1 day	Male on lake-fly diet	1.0	-5.0	13.0	$Z = 1.556$, $P = 0.120$
Male	Female on blood diet for 14 days	Female on blood diet for 1 day	6.0	-2.0	18.0	$Z = 2.554$, $P = 0.011$
Female	Male on blood diet for 14 days	Male on blood diet for 1 day	10.0	-1.0	18.0	$Z = 3.765$, $P < 0.001$
Male	Female on blood diet for 28 days	Female on blood diet for 14 days	5.0	-8.0	15.0	$Z = 2.273$, $P = 0.023$
Female	Male on blood diet for 28 days	Male on blood diet for 14 days	0.0	-13.0	16.0	$Z = 0.554$, $P = 0.580$

Table 3.3. Scores for *Evarcha culicivora* when tested for effect of switching source-spider diet from blood to lake flies. All test and source spiders virgins. For each row, $n = 50$. Score: time spent near source spider 2 minus time spent near source spider 1

Test spider	Source Spider 1	Source Spider 2	Median score	First quartile	Third quartile	Wilcoxon test
Male	Female on blood diet	Female on lake-fly diet for 1 day	12.0	0.0	24.0	$Z = 3.820$, $P < 0.001$
Female	Male on blood diet	Male on lake-fly diet for 1 day	5.5	-2.0	22.0	$Z = 3.051$, $P = 0.002$
Male	Female on lake-fly diet for 1 day	Female on lake-fly diet for 14 days	4.0	-7.0	18.0	$Z = 2.597$, $P = 0.009$
Female	Male on lake-fly diet for 1 day	Male on lake-fly diet for 14 days	5.5	-9.0	26.0	$Z = 2.635$, $P = 0.008$

Table 3.4. Scores for *Evarcha culicivora* when tested for effect of fasting. All test and source spiders virgins. For each row, $n = 50$. Score: time spent near source spider 2 minus time spent near source spider 1

Test spider	Source Spider 1	Source Spider 2	Median score	First quartile	Third quartile	Wilcoxon result
Male	Female on blood diet	Female on blood diet then fasted 7 days	7.0	2.0	17.0	$Z = 3.377$, $P = 0.001$
Female	Male on blood diet	Male on blood diet then fasted 7 days	12.0	0.0	20.0	$Z = 3.939$, $P < 0.001$
Male	Female on blood diet then fasted 7 days	Female on blood diet then fasted 14 days	10.0	1.0	19.0	$Z = 4.113$, $P < 0.001$
Female	Male on blood diet then fasted 7 days	Male on blood diet then fasted 14 days	10.5	-1.0	27.0	$Z = 3.605$, $P < 0.001$

Chapter 4

The effect of draglines from other salticids on *Evarcha culicivora*'s behaviour

Abstract

Evarcha culicivora, a jumping spider from the Lake Victoria region of East Africa, can identify conspecifics on the basis of vision alone and on the basis of odour alone. Here I investigate for the first time how this species uses cues associated with draglines. Experimental findings imply that males can determine whether draglines are derived from conspecific females. In choice tests, they show a preference for the draglines of virgin instead of already-mated females and for larger instead of smaller females. They also discriminate between draglines of large and small conspecific males. Virgin females show a preference for draglines of larger males, but mated females show a preference for draglines of smaller males. There is also experimental evidence that *E. culicivora* identifies the draglines of a particular predator, *Portia africana*.

Introduction

In Chapters 2 and 3 I showed that *Evarcha culicivora* has a pronounced ability to use olfaction, discriminating same-sex from opposite-sex conspecifics, and even identifying the diet of potential mates, by odour cues alone. In this chapter, I review some preliminary work that might be envisaged as a step toward extending what we know about *E. culicivora*'s use of chemoreception. When moving about their environment,

salticids routinely trail behind them silk lines called 'draglines' (see Figs. 4.1 and 4.2). Here I consider the information *E. culicivora* might pick up from contact with draglines.

There has been very little research on salticid olfaction, and so my research in Chapters 2 and 3 is particularly unusual for the literature to date. However, there have been many studies showing that salticid females leave species- and sex-identifying chemical cues (i.e., 'signpost signals') on their draglines and that part of the male's mating strategy is to identify these draglines (Clark & Jackson, 1995; Jackson, 1987; Pollard et al., 1987; Taylor, 1998; see also references in Huber, 2005). That the relevant cues are detected by contact chemoreception is supported by experiments where silk loses its effectiveness after being soaked in ethanol or left in the open for a week (Jackson, 1987).

One of my hypotheses is that *E. culicivora* males can determine whether draglines are derived from conspecific females. However, I also consider some hypotheses that are based more specifically on the unusual things we know about the biology of *E. culicivora*. Knowing that *E. culicivora* is a species in which mutual mate choice is pronounced (Cross et al., 2008), where both sexes make mate-size choices by sight (Cross et al., 2007), I will consider whether both sexes of this species identify the draglines of opposite-sex conspecific individuals and whether they make mate-size choices on the basis of cues from draglines. I will also investigate whether *E. culicivora* can use cues from draglines for determining the size of same-sex conspecific individuals. Moreover, I will consider whether, while relying on dragline-associated cues, potential mates that are virgins can be discriminated from potential mates that have mated previously.

Another hypothesis is that *E. culicivora* uses dragline-associated cues for determining whether a particular predator, *Portia africana*, is in the vicinity. *P. africana* is a special predator because it is araneophagic (i.e., its preferred prey is other spiders, including *E. culicivora*; Jackson, unpubl. data) and is common in *E. culicivora*'s habitat of the Lake Victoria region of East Africa. More specifically, my hypothesis is that *E. culicivora*'s ability to identify the draglines of *P. africana* is highly specific to this particular salticid species (a special predator), not a general ability that pertains to other salticid species in general or even another species of *Portia*.

Materials and Methods

Laboratory work was carried out at the Thomas Odhiambo Campus of the International Centre of Insect Physiology and Ecology (ICIPE) (Mbita Point, western Kenya) and at the University of Canterbury (Christchurch, New Zealand) using cultures established from individuals collected at Mbita Point. For standard salticid-laboratory procedures, see Cross et al. (2008) (Appendix 6). All testing was carried out between 0800 h and 1300 h (laboratory photoperiod 12 light:12 dark, lights on at 0700 h). Spiders were tested, and source spiders were used, 3–4 days after they were last fed.

Test spiders were adult males and adult females of *E. culicivora* that had reached maturity 7–14 days before tested and, before use in experiments, had no experience with any draglines of the types I used. Unless stated otherwise, all test spiders were of standardised size (5 mm; see Cross et al., 2007) and were virgins (i.e., had not encountered any conspecific individuals before tested). No draglines and no spider that was a dragline source was used more than once in the same experiment and, unless the test spider was a female that had been tested both before and after mating

(each test on successive days), no test spider was used more than once in the same experiment.

In Experiment 1, the source spiders (*Evarcha culicivora* females) were of different mating status (virgin and mated). In Experiments 2 and 3, the test spiders and source spiders (*E. culicivora* males and females) were of different size (small: 3 mm; medium: 5 mm; large: 6 mm). The source spiders in Experiment 4 were all virgin females of *Portia africana* (from Kenya; body length 10 mm), *Portia fimbriata* (from Malaysia; body length 10 mm) and *Hypoblemum albovittatum* (from New Zealand; body length 8 mm).

The testing apparatus was a transparent plastic Petri dish (diameter 90 mm) divided in to two equal-size sections by a partition (1-mm thick dark-green paper card) positioned vertically across the centre of the dish and secured with sticky tape. The source spider was restricted to one side of this partition ('side 1'; whether on left or right determined at random) for 1 h, during which time it moved around, depositing draglines. The other side of the dish ('side 2') was left empty ('control') or it was occupied by a different source spider.

Unlike the common practice in experiments with lycosid spiders (e.g., Persons et al., 2002), the Petri dishes used in the present experiments were not lined with blotting paper (i.e., draglines were deposited on the dish surface). Lycosids tend to remain on the floor of a dish covered with paper, but salticids are more inclined to walk on all surfaces, and this is why a paper lining is not very effective for dragline collection when using salticids.

In Experiment 1, the sides of the dish were referred to as 'female side', 'virgin-female side' and 'mated-female side'. In Experiments 2 and 3, the sides of the dish were 'small-female side' and 'large-female side', as well as 'small-male side',

'medium-male side' and 'large-male side'. In Experiment 4, the sides of the dish were '*P. africana* side', '*P. fimbriata* side' and '*H. albovittatum* side'.

After the 1-h pre-test period, the source spider(s) and partition were removed. Immediately after removing the source spider and partition, a test spider that had been kept in a vial for 5 min beforehand was introduced to the centre of the Petri dish (brushed gently using a soft paint brush). Data recording began 1 min after the test spider was put into the dish, the rationale for this 1-min waiting period being that test spiders tended to behave erratically immediately after they were introduced into the dish. Sometimes they froze and other times they moved rapidly around through the Petri dish, but they moved calmly after 1 min.

Tests lasted for 30 min and during this time I recorded how long the test spider stayed on each side of the dish. Male test spiders sometimes displayed after contacting the silk and, in these instances, I recorded the side of the dish where the male was located when he first displayed. I also calculated the percentage of the total time spent displaying on each side of the dish. At the end of the test, the test spider was removed and the Petri dish was cleaned with 80% ethanol and then dried.

As my data often did not meet the assumptions required for parametric data analyses, I used Wilcoxon tests for paired comparisons (null hypothesis: time spent on side 1 matched time spent on side 2). A score was calculated for each test spider by subtracting time spent on side 1 from time spent on side 2 (positive score: spider spent more time on side 1; negative score: spider spent more time on side 2). Using Mann-Whitney *U*-tests, I also compared the scores for different groups of test spiders (null hypothesis: scores for one group of test spiders matched scores for another group of test spiders). Unless stated otherwise, Wilcoxon-test results are in Tables 4.1 and 4.2, whereas Mann-Whitney test results are in the text. Data for males that displayed in the

Petri dishes were analysed using chi-square tests of goodness of fit and chi-square tests of independence. Bonferroni adjustments were applied whenever there was repeated analysis of the same data sets. For details about statistical procedures, see Howell (2002).

Results

Behaviour of Evarcha culicivora *when in contact with draglines*

Two distinctive categories of behaviour were relevant, palpating draglines (which happened often) and displaying (which happened only occasionally). Palpating draglines is described here for the first time. 'Display', however, refers to behaviour used during courtship that has already been defined and described in detail elsewhere (Cross et al., 2008; see Appendix 6). When palpating draglines, the spider first contacted silk lines with its legs I, raised these legs, pulling these draglines up, and then held the draglines close to its palps (for information on anatomical details, see Fig. 1 in Cross et al., 2008; Appendix 6). While holding the silk this way, the spider moved its palps up-and-down and forward-and-backward in one direction, followed by a momentary pause and then by movement in the other direction (c. 1–3 cycles per s in bouts of c. 5 s; amplitude of movement, 0.5–1 mm). The tarsi of the palps made repeated contact with the draglines. After palpating for a few seconds to several minutes, the spider lowered its legs I. Often it then moved to a new location and palpated again. When spiders displayed, this was after bouts of palpating.

During courtship, spiders typically step with palps (i.e., move the two palps up and down in an alternating fashion, as if stepping in the air; males only), posture with legs erect or hunched, dance and twitch their abdomens, and these behaviour patterns were also sometimes seen when spiders were on draglines. The male's displaying in

tests with draglines typically followed an initial sequence of palpating with an intervening period of palp stepping before he began moving actively around the Petri dish, twitching his abdomen and posturing with legs erect during pauses between steps. Females in dragline tests typically postured with hunched legs when they displayed.

Do males prefer draglines of opposite-sex conspecific individuals (Experiment 1)?

Males spent more time on the female side of the dish than on the control side (Table 4.1). The amount of time males stayed on the virgin-female side was not significantly different from the amount of time on the mated-female side. However, the percentage of time males displayed while on the virgin-female side (median = 1.4%; first quartile = 0.65%; third quartile = 2.35%) was significantly higher than the percentage of time males displayed on the mated-female side (median = 1.3%; first quartile = 0.25%; third quartile = 2.05%) (Wilcoxon test: $Z = 2.39$, $p = 0.017$). Moreover, 22 males initiated displaying on the virgin-female side, whereas only 10 males initiated displaying on the mated-female side ($\chi^2 = 4.50$, $p = 0.034$). This suggests that, for males, draglines from virgin females are more attractive than draglines from mated females.

Can males discriminate between draglines of different size conspecific individuals (Experiment 2)?

Males spent significantly more time on the large-female side than on the small-female side of the dish (Table 4.1). There was no significant difference between the percentage of time males displayed on the large-female side (median = 2.25%; first quartile = 1.55%; third quartile = 2.75%) and the percentage of time males displayed

on the small-female side (median = 2.05%; first quartile = 1.30%; third quartile = 2.75%) (Wilcoxon test: $Z = 0.743$, $p = 0.458$). However, 22 males initiated displaying on the large-female side whereas only five initiated displaying on the small-female side ($\chi^2 = 10.704$, $p = 0.001$).

When test-spider size varied but male source-spider size was standardised, small-male test spiders spent significantly less time on the medium-male side than on the control side. However, for medium-male test spiders and for large-male test spiders, the amount of time spent on the medium-male side was not significantly different from the amount of time spent on the control side (Table 4.1). When test-spider size was standardised but source-spider size varied, the amount of time medium males spent on the male side was not significantly different from the amount of time they spent on the control side, regardless of whether the source spider was small or large (Table 4.1).

Can females discriminate between draglines of different size conspecific males (Experiment 3)?

Regardless of whether they were virgins ($N = 22$) or had mated ($N = 11$) before the test, the amount of time female test spiders spent on the large-male side was not significantly different from the amount of time spent on the small-male side (Table 4.1). However, when I compared data, for only the females that had mated ($N = 11$), before and after mating, the amount of time they spent on the small-male side before mating was significantly less than the amount of time they spent on the small-male side after mating (Wilcoxon test: $Z = 2.045$, $p = 0.041$).

Can males identify the draglines of Portia africana*, a predator (Experiment 4)?*

Males spent significantly more time on the control side than on the *P. africana* side, but the amount of time they spent on the *P. fimbriata* or the *H. albovittatum* side was not significantly different from the amount of time they spent on the control side (Table 4.2).

Displaying when in contact with draglines

When there were draglines on one side of the Petri dish and no draglines on the other side (control), 21 out of 30 males displayed when the draglines were from conspecific females. They never displayed when the draglines were from conspecific males or from heterospecific salticids (display while on female versus male draglines: $\chi^2 = 51.86$, $p<0.001$; female versus *P. africana*: $\chi^2 = 32.31$, $p<0.001$; female versus *P. fimbriata*: $\chi^2 = 32.31$, $p<0.001$; female versus *H. albovittatum*: $\chi^2 = 32.31$, $p<0.001$).

Comparison of scores

Scores for males tested with female draglines (paired with the control) were significantly higher than scores for males tested with other dragline types (paired with the control) (female versus conspecific male (medium size): $Z = 4.01$, $p<0.001$; female versus *P. africana*: $Z = 4.82$, $p<0.001$; female versus *P. fimbriata*: $Z = 3.79$, $p<0.001$; female versus *H. albovittatum*: $Z = 3.53$, $p<0.001$). Scores for males tested with medium-male draglines were not significantly different from scores for males tested with *P. africana* draglines ($Z = 0.65$, $p = 0.515$), *P. fimbriata* draglines ($Z = 0.61$, $p = 0.543$), or *H. albovittatum* draglines ($Z = 1.31$, $p = 0.190$).

Scores for males tested with *P. africana* draglines were not significantly different from scores for males tested with *P. fimbriata* draglines ($Z = 1.49$, $p = 0.137$)

or *H. albovittatum* draglines ($Z = 2.12$, $p = 0.068$). Moreover, scores for males tested with *P. fimbriata* draglines were not significantly different from scores for males tested with *H. albovittatum* draglines ($Z = 0.44$, $p = 0.657$).

When tested with draglines from medium *E. culicivora* males, scores for large male test spiders were significantly higher than scores for small male test spiders ($Z = 3.10$, $p = 0.004$) and for medium male test spiders ($Z = 2.49$, $p = 0.026$). However, scores for small test spiders were not significantly different than scores for medium test spiders ($Z = 0.81$, $p = 0.417$). Also, scores for medium males tested with draglines from small *E. culicivora* males were not significantly different from scores for medium males tested with draglines from large *E. culicivora* males ($Z = 0.41$, $p = 0.681$).

When tested with draglines from large and small conspecific males, scores for virgin females were significantly higher than scores for mated females ($Z = 2.16$, $p = 0.031$).

Discussion

One of the most basic conclusions suggested by these preliminary findings is that, for *E. culicivora*, the draglines of opposite-sex conspecifics are salient. Males can discriminate between conspecific female and male draglines as well as discriminate between conspecific female draglines and draglines of other salticid species. Moreover, 86.96% of the males began displaying after contacting the silk of an opposite-sex conspecific, but none began displaying after contacting other kinds of draglines, this being further evidence that the male identifies female draglines as coming from a potential mate. These findings are nothing particularly new, as there is a sizeable number of salticid species for which it is now known that the draglines of

females elicit courtship by conspecific males (Huber, 2005; Jackson, 1987; Jackson & Pollard, 1997; Pollard et al., 1987).

Yet there are more novel, and subtle, conclusions suggested by the findings in this chapter. Apparently *E. culicivora* can discriminate between draglines left by conspecific individuals of different sizes, whether they are of the opposite or same sex. An obvious next step will be to determine precisely what properties of draglines are correlated with the body size of the spider from which the draglines originated. It is not obvious how or why there would be a reliable relationship between spider size and the chemical characteristics of draglines. Perhaps thread thickness or volume is positively correlated with spider size and perhaps test spiders can determine these characteristics while palpating, although exactly how they might be able to do this is not immediately apparent.

However, the findings in this chapter seem to be telling us that *E. culicivora* can make mate-size decisions on the basis of draglines alone in ways that parallel the results from an earlier study where *E. culicivora* could see potential mates (Cross et al. 2007). In this chapter, as with Cross et al. (2007), when males and females are virgins they prefer larger opposite-sex conspecifics, but after females have mated they prefer smaller males. In the future, it would be especially interesting to test whether spiders also choose the draglines of opposite-sex conspecifics on the basis of diet, with draglines from spiders that have recently fed on blood being more attractive than draglines from spiders that have not recently fed on blood.

Moreover, *E. culicivora* males may discriminate between draglines of other males that differ in size. Smaller males in particular appear to avoid draglines from bigger males, whereas larger males may actually be attracted to draglines from smaller males, perhaps for a chance to prey on them. Studies with other species have

shown that there is a trend for larger salticid males to have an advantage in contests with other males (Faber & Baylis, 1993; Jackson & Cooper, 1991; Taylor et al., 2001; Wells, 1988), and we are accustomed to the idea of salticid males using vision to judge a rival's size. It certainly raises some interesting questions if male body size is revealed by the signpost signals associated with draglines. For example, if these signals can repel potential rivals, what keeps cheating under control? Can small individuals exploit this system by dishonestly advertising their size, indicating with signpost signals on their draglines that they are larger than they really are?

Also begging for follow-up research is how *E. culicivora* seems to avoid the draglines of another salticid that is known to be a potential predator in its habitat (Jackson, unpubl. data). Salticids in general may be potential predators of other salticids, but *P. africana* may be a particularly serious problem for *E. culicivora*. *P. africana*, like all species from the genus *Portia*, single out other spiders as preferred prey (Jackson & Pollard, 1996; Jackson & Wilcox, 1998). At this stage, it is still too soon to draw strong conclusions, but there was nothing in my findings to suggest that *E. culicivora* avoids the draglines from the other two salticid species I used. One of these other species was actually another species that prefers spiders as prey, being another *Portia* species, *P. fimbriata*. This suggests that *E. culicivora* does not pick up cues from these draglines that identify the spider as simply being from the genus *Portia* and as such a predator to be avoided. *P. fimbriata* is native to tropical regions in Asia, New Guinea and Australia, not Africa (Jackson & Pollard, 1996). The findings in this chapter suggest that there may be a signature added to draglines indicating that the origin of the silk is specifically the predator from the same habitat. This signature, whatever it might be, does not appear to be a metabolic product from feeding on *E. culicivora*, as the individuals of *P. africana* used in my experiment were

from laboratory culture and had never made a meal of or had any other encounter at all with *E. culicivora*. However, it would certainly be interesting to investigate whether *E. culicivora* is especially inclined to avoid draglines from *P. africana* individuals that have recently fed on *E. culicivora* (e.g., see Turner, 2008).

There are many studies on how animals detect the chemical stimuli from potential predators, and many of these studies, but far from all of them, come from aquatic systems (e.g., Brown et al., 2006; Ferrari et al., 2008; Gonzalo et al., 2007). This literature will provide a rich source of ideas and hypotheses to consider in future research on *E. culicivora*. There are even studies showing that spiders belonging to another family, the Lycosidae, detect other spider species that are predators and, on this basis, take defensive measures (Bell et al., 2006; Persons et al., 2002; Rypstra et al., 2007). We know little about the defensive measures taken by *E. culicivora* upon detecting draglines from *P. africana*, but this literature will provide a rich source of hypotheses that might be applied to *E. culicivora*.

Some basic improvements in the apparatus and testing procedures will be helpful. It was difficult to standardise activity levels of test spiders, especially immediately after they entered the Petri dish, with some spiders remaining motionless and others becoming very active. A step toward solving these problems might be to have the test spider enter, via a vial, through a hole in the centre of the floor of the Petri dish, allowing it, without prodding, to walk up into the apparatus. This might be a way of ensuring that test spiders enter the Petri dish calmly and for ensuring that they enter precisely in the centre of the dish.

Moreover, it may be especially useful to determine the information that *E. culicivora* can acquire from draglines compared to the information it can acquire from odour in the absence of contact with draglines. The findings in this chapter may be

hinting that draglines give the spider types of information that are not so accessible by olfaction alone. For example, from the olfactometer experiments there was no evidence that *E. culicivora* males discriminate between the odour of virgin and mated opposite-sex conspecific source spiders (Cross & Jackson, in press; see Chapter 2), but the preliminary evidence in the present chapter suggests that they may make this discrimination when they have access to draglines.

We should also address an issue that is rarely acknowledged in the literature on spider behaviour. There have been many experimental studies based on giving spiders an opportunity to contact draglines and it is routine to conclude that the spider's behaviour is mediated by contacting chemical cues in the silk. However, it is not so simple to rule out an alternative hypothesis that olfaction is actually mediating the behaviour observed (i.e., instead of contacting the silk being critical, the spider may be detecting volatile compounds from the silk). With an olfactometer, the possibility of contacting another spider or its draglines can be eliminated, but when contact is permitted, eliminating the possibility of olfaction will be a much greater challenge.

However, the apparatus and testing procedure adopted in this chapter, plus the behaviour observed, suggests that olfaction is unlikely to explain the findings. The apparatus was a small, closed Petri dish and, in this confined space, it seems unlikely that any odour from particular kinds of draglines would have remained sufficiently localized to account for the findings I got. In particular, the male, whenever he displayed, was standing on the side of the dish where there were draglines from a conspecific female. It is also interesting that *E. culicivora* usually palpated immediately before displaying. Although there is more to learn about this behaviour, it seems that contacting the silk is an important preliminary to displaying.

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Fig. 4.1. *Evarcha culicivora* female (facing right) on *Lantana camara*, moving to a lower part of the plant while depositing a dragline from her spinnerets. Photograph: R. Jackson.

Fig. 4.2. *Evarcha culicivora* male on *Lantana camara* inflorescence (on right) moving across on draglines to another inflorescence where female (on left) is located. Draglines attached to both inflorescences. Photograph: R. Jackson.

Table 4.1. Results for dragline tests for male and for female test spiders (Experiments 1–3). Unless stated otherwise, test spiders and source spiders were virgins and of standard body length (i.e., 5 mm).

Experiment	Test spider	N	Source spider side 1	Source spider side 2	Median score	First quartile	Third quartile	Wilcoxon result
1	Male	30	Female	Blank	417	112	810	$Z = 3.630$, $p<0.001$
	Male	34	Female	Female (mated)	132	-162	470	$Z = 1.325$, $p = 0.185$
2	Male	28	Female (large)	Female (small)	339	-26	810	$Z = 3.006$, $p = 0.003$
	Male (small)	12	Male	Blank	-287	-489	8	$Z = 2.353$, $p = 0.019$
	Male (medium)	25	Male	Blank	-210	-412	94	$Z = 1.771$, $p = 0.077$
	Male (large)	19	Male	Blank	170	42	364	$Z = 1.811$, $p = 0.070$
	Male	18	Male (small)	Blank	-92	-436	238	$Z = 0.762$, $p = 0.446$
	Male	18	Male (large)	Blank	-180	-366	0	$Z = 1.752$, $p = 0.080$
3	Female	22	Male (large)	Male (small)	222	-150	550	$Z = 1.932$, $p = 0.053$
	Female (mated)	11	Male (large)	Male (small)	-256	-460	218	$Z = 1.067$, $p = 0.286$

Table 4.2. Results for dragline tests for male test spiders (Experiment 4). Source spiders were all females. Test spiders and source spiders were virgins and of standard body length (see text for details). One side of Petri dish contained draglines from one source spider; other side of Petri dish was left blank.

Test spider	N	Source spider side 1	Median score	First quartile	Third quartile	Wilcoxon result
Male	30	*Portia africana*	-221	-442	10	$Z = 3.157$, $p = 0.002$
Male	30	*Portia fimbriata*	-69	-368	146	$Z = 1.038$, $p = 0.299$
Male	30	*Hypoblemum albovittatum*	-92	-254	188	$Z = 0.391$, $p = 0.696$

Chapter 5

Complex display behaviour on two plant species by *Evarcha culicivora*, an East African mosquito-eating jumping spider

Abstract

Evarcha culicivora, an East African jumping spider (Salticidae), is unusual because it feeds indirectly on vertebrate blood by choosing blood-carrying mosquitoes as preferred prey, and it also associates with two particular plant species, *Lantana camara* and *Ricinus communis*. Previous work had also highlighted *E. culicivora*'s exceptionally complex display repertoire. In contrast to most other salticids that have been studied, the males and the females of *E. culicivora* are both active at initiating and sustaining courtship, and both sexes are cannibalistic. However, male-female interactions of *E. culicivora* are especially complex when encounters are in the foliage of *L. camara* and *R. communis* and these interactions also take significantly longer than when individuals meet in empty cages.

Introduction

Most spiders have eyes that lack the structural complexity required for acute vision (Homann, 1971; Land, 1985), but salticids have a pair of distinctively large forward-facing anterior-medial eyes that support exceptional spatial acuity (Blest et al., 1990; Harland & Jackson, 2004; Land, 1969a, 1969b; Williams & McIntyre, 1980). Not surprisingly, the most elaborate vision-based display behaviour known for spiders (Foelix, 1996), and among the most elaborate ever described for any animal group, is

found in this family (Crane, 1949; Jackson, 1982a; Jackson & Pollard, 1997; Maddison & Hedin, 2003).

Evarcha culicivora (Araneae, Salticidae) is an unusual predator because it feeds indirectly on vertebrate blood by choosing blood-carrying mosquitoes as preferred prey (Jackson et al., 2005; Nelson & Jackson, 2006; Nelson et al., 2005) and it is also an unusual spider because it associates with, and feeds on the nectar of, *Lantana camara* and *Ricinus communis*, plant species that grow wild in the same habitat. *Ricinus communis* (family Euphorbiaceae) (Fig. 5.1) is native to tropical Africa (Cronk & Fuller, 1995), but *Lantana camara* (family Verbenaceae) (Fig. 5.2) is native to tropical and subtropical America and has been introduced to many parts of the world as an ornamental plant (Ghisalberti, 2000), including East Africa.

E. culicivora's association with *L. camara* and *R. communis* is still currently poorly understood but, aside from being potential sources of nectar, these plants may also play an important role for *E. culicivora* during intraspecific interactions. For my MSc, I provided a detailed description of the behaviour patterns used by *E. culicivora* during interactions, but these interactions were all staged in empty cages. In this chapter, however, I provide a mainly qualitative summary of how *E. culicivora* interact on *L. camara* and *R. communis*.

The work in Chapters 2–4 indicated that *E. culicivora*'s mate-choice behaviour is exceptionally complex. However, by comparing how *E. culicivora* interact on *L. camara* and *R. communis* instead of in empty cages, I highlight in this chapter another unique facet of this salticid's behaviour. The work in this chapter is part of important ongoing work on how *E. culicivora*'s unusual diet and its unusual affinity for particular plant species interrelate with mate-choice behaviour, display function, tactical design and selective attention.

The summary included here was published within a much larger article (Cross et al., 2008) in *New Zealand Journal of Zoology*. This published paper (see Appendix 6) contains definitions of behaviour categories that may be useful to refer to while reading the summary below.

Materials and Methods

Laboratory work was carried out at the Thomas Odhiambo Campus of the International Centre of Insect Physiology and Ecology (ICIPE) (Mbita Point, western Kenya) and at the University of Canterbury (Christchurch, New Zealand) using cultures established from individuals collected at Mbita Point. For standard salticid-laboratory procedures, see Cross et al. (2008) (Appendix 6) and Jackson & Hallas (1986). For anatomical details that are important for describing behaviour, see Fig. 1 in Cross et al. (2008) (Appendix 6).

My summaries are for interactions between individuals that were similar in size (i.e., body lengths matched to the nearest mm). Hereafter, the shorter expressions 'male' and 'female' will be used for 'adult male' and 'adult female'. Earlier convention (Jackson & Hallas, 1986) is adopted for indicating frequencies of occurrence: "usually", "often", "typically" and "typical" indicate c. 80% or more; "sometimes" and "occasionally" indicate 20–80%; "infrequently", "rarely" and "on rare occasions" indicate 20% or less.

By definition, an encounter began when one spider fixated the gaze of its principal-eye corneas on the other spider and then either maintained fixation for at least 30 s or else began displaying. When an encounter failed to occur within 30 min, the test was terminated. By definition, interactions began when the spiders began to adopt display behaviour (for a full summary, see Cross et al., 2008; Appendix 6),

whereas interactions ended when one spider fled and the other spider failed to watch or follow it for the next 60 s.

Instead of staging encounters inside bare cages ('no-plant tests'), as in earlier salticid studies (Jackson & Pollard 1997), I staged male-male, female-female and male-female interactions on *L. camara* and *R. communis* ('plant tests'). Plant tests were staged in two ways: 1) leaves and flowers of *L. camara* were placed inside a cage; 2) the spiders were put together on potted *L. camara* or *R. communis* plants sitting on a laboratory bench in the open. Individuals did not have prior exposure to these plants before being used in tests. All sex-age classes readily walked on to the cuttings and on to the potted plants, and *E. culicivora* was especially inclined to settle on the flowers of *L. camara*, seeming reluctant to leave even when prodded aggressively with a small paint brush.

For staging an interaction inside a cage, with or without a plant present, one spider (the 'intruder') was introduced through a hole (diameter 10 mm; plugged with rubber stopper) into a cage already occupied by another spider (the 'resident'). For staging an interaction on a plant in the open, first the resident was put on the plant and then, 60 min later, the intruder was put on the plant 15–20 mm away from the resident.

Individuals were chosen at random from the laboratory stock, but no individual was used more than once in any one type of interaction. Whether an individual spider was the intruder or the resident was decided at random.

I also recorded the duration of a subsample of interactions and, using Mann-Whitney *U*-tests (see Howell, 2002), I compared the interaction durations of spiders that met on plants with the interaction durations of spiders that met in empty cages.

Results

Observed behaviour

Previous work (see Cross et al., 2008; Appendix 6) had shown that male-female interactions of *E. culicivora* are exceedingly complex and variable, with both the male and the female displaying actively and both being prone to initiating courtship. Although many of the particular behaviour categories adopted by *E. culicivora* have close parallels with other salticid species, what sets *E. culicivora* apart is that its display repertoire includes exceptionally many behaviour categories, and these are combined in the most complex and variable sequences ever reported for a spider (see Cross et al., 2008; Appendix 6).

All the behaviour categories seen during interactions in bare cages were also seen during interactions on *L. camara* and *R. communis*, and vice versa. Sequences during interactions when on *L. camara* and *R. communis* were also in basic respects similar to interactions when the spiders were in bare cages. However, interactions on *L. camara* and *R. communis*, especially male-female interactions, were distinctive because of much greater variability in the performance of individual categories of behaviour and in sequencing.

With the two spiders moving about actively through the dense inflorescences (especially on *L. camara*), each spider's view of, and path to, the other spider was routinely occluded by the flowers and other vegetation (Figs. 5.3 and 5.4). It was common for one spider to leap about on the plant, with the other spider usually orienting toward the leaping spider and this spider's orienting response, in turn, attracting the attention of the spider that had been leaping. Another impression I got from observation was that sometimes, when a male saw a female before she saw him,

he deliberately hid behind leaves and stems, or in the inflorescence, until the female passed by, and then he suddenly emerged and began posturing (Fig. 5.5) or dancing.

In bare cages, when one spider departed or fled from the other spider, this was primarily by walking or running, but spiders on plants often shuffled or dodged out of the way by quickly moving under vegetation, leaping from one part of the plant to another or dropping on a dragline to a lower part of the plant. There were also instances of one spider dropping on a dragline from higher up in the vegetation toward another spider lower down, with males approaching females this way more often than vice versa and sometimes posturing as they did so.

It was routine for one spider to display at another spider that was facing up, down, left, right or at almost any conceivable angle (Fig. 5.4), with the displaying spider often tilting so as to achieve closer approximation to being head-on and oriented in the same plane with the other spider.

Dancing was especially complex on plants. While moving in an arc during a zigzag dance, for example, a male sometimes had to maintain his footing on a slender shred of vegetation (Fig. 5.6), make repeated leaps from flower to flower, and so forth. The male's dancing path sometimes took him one or more times from the top side to the bottom side of a leaf and back, or vice versa. Although combining zigzag dancing with linear dancing was uncommon when in bare cages, males often combined zigzag dancing with linear dancing when on plants. For example, males sometimes linear danced by moving up and down the stalk of a plant after zigzag dancing on a flower or leaf.

When in the vegetation, mounting and mating often appeared to be especially challenging. Sometimes the male began pre-mount tapping while reaching from a part of the vegetation where he was standing to another part where the female was

standing (Fig. 5.7), with mounting being achieved not by simply walking forward over the female, as was routine in bare cages, but instead by moving over the female from some other angle. When the female was buried deep within an inflorescence, it often seemed impossible for males to mount (Fig. 5.8), yet males tried and sometimes succeeded in reaching over to the female's rotated abdomen to engage a palp, sometimes with a leaf or a stem running between the male and female. Often, when the female was in an inflorescence, she came out and the two mated on a less cluttered space on the plant (e.g., on a flower top).

Interaction durations

For male-female interactions, durations on *Lantana camara* were not significantly different from durations on *Ricinus communis* ($Z = 0.74$, $p = 0.46$; Fig. 5.9), so I pooled these data ("on plants"). Male-female interactions were significantly longer on plants than in bare cages ($Z = 8.73$, $p<0.001$).

For male-male (Fig. 5.10) and for female-female (Fig. 5.11) interactions, durations on *Lantana camara* were again not significantly different from durations on *Ricinus communis* (males: $Z = 1.48$, $p = 0.139$; females: $Z = 0.89$, $p = 0.38$), and so I pooled these data. Using the pooled data, male-male and female-female interactions were significantly longer on plants than in bare cages (males: $Z = 6.86$, $p<0.001$; females: $Z = 3.54$, $p<0.001$).

Discussion

Within the family Salticidae, males typically display more persistently than females during male-female interactions (Jackson & Pollard, 1997), with females tending to alternate between watching the male and moving a short distance away. Salticid

females are typically envisaged as determining whether mating takes place (i.e., it is primarily the female that does the choosing) by either allowing or not allowing the male to approach, mount and copulate. This is consistent with the prevailing trend in the animal kingdom as a whole (Andersson, 1994; Bradbury & Anderson, 1987).

However, *Evarcha culicivora* appears unconventional because both the male and the female of this species display actively and both sexes are prone to initiating courtship. From other studies, there is evidence that both sexes of *E. culicivora* exercise pronounced mate-choice behaviour, choosing on the basis of the body size of potential mates (Cross et al., 2007) and also on the basis of the odour potential mates acquire by feeding on blood-carrying mosquitoes (see Chapter 3).

Selective attention is an often neglected topic in the mate-choice literature (see Dukas, 2002), but much of *E. culicivora*'s display behaviour may function in attracting the attention, and sustaining the attention, of potential mates. Interaction complexity, and especially the adoption of displays that are rich in movement, may function in part as anti-habituation mechanisms (Jackson, 1982b). Resurrecting long-forgotten, yet still important, ideas from the literature on bird song, *E. culicivora*'s display behaviour might be explained in part as each individual striving to avoid the other individual's 'monotony threshold' (see Hartshorne, 1956, 1958).

The variability of *E. culicivora*'s display behaviour may be especially relevant when considered in the context of courting and mating in the dense inflorescences of plants, especially *L. camara* and *R. communis*, where the surfaces on which the interacting spiders move about is complex and visual obstructions intervene between the spiders as they exchange signals. *E. culicivora*'s display behaviour often appeared more exaggerated when individuals met on plants, and perhaps being predisposed to meet on the foliage of plants functions as a means by which spiders challenge each

other's ability to orchestrate complex display behaviour. Setting up challenges of this sort might function in the context of intersexual selection (see Andersson, 1994).

Interactions on plants were also longer than in empty cages, further highlighting the challenges that *E. culicivora* faces when interacting with other individuals in this complex environment. Yet a particularly salient aspect of *E. culicivora*'s behaviour on the plants was the tendency for individuals to move abruptly, such as by leaping, which often appeared to attract the attention of the other spider. This may indicate that *E. culicivora* has an innate strategy to compensate for the visual obstructions in this environment.

Although there is still more that needs to be discovered about *E. culicivora*'s association with *L. camara* and with *R. communis*, my observations suggest that these plants might play an important role as sites for encountering potential mates. Once the spiders were on the plants, they appeared reluctant to leave, suggesting that *L. camara* and *R. communis* are attractive to *E. culicivora* and that these plants are an important part of this species' biology. The next step in determining whether *L. camara* and *R. communis* are important to *E. culicivora* is by investigating whether the odours of these two plant species are particularly salient to this salticid species. I consider this in Chapter 6.

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Fig. 5.1. *Ricinus communis* flowers. Photograph: R. Jackson.

Fig. 5.2. *Lantana camara* inflorescence.

Fig. 5.3. *Evarcha culicivora* male (on right) on *Lantana camara* flowers with legs I erect in extended position 4. Female departing by walking away (cephalothorax between two flowers; only abdomen visible in photograph). Photograph: R. Jackson.

Fig. 5.4. Male-female pair of *Evarcha culicivora* interacting on *Ricinus communis*. Female partly obscured by vegetation (below). Photograph: R. Jackson.

Fig. 5.5. *Evarcha culicivora* male and female, each on a different *Lantana camara* flower. Male (upside down, on left). Female (on flower on right) walking (abdomen in view). Male, partially hidden under flowers, emerges and postures with legs in erect position 3. Photograph: R. Jackson.

Fig. 5.6. *Evarcha culicivora* male zigzag dancing while on a *Ricinus communis* flower. Legs I erect in position 3. Stepping to his left, with abdomen tilted to his right. Female is deeper in vegetation below male (not visible in photograph). Male leans down to face female. Photograph: R. Jackson.

Fig. 5.7. *Evarcha culicivora* male (above) standing on *Lantana camara* flower and pre-mount tapping female that is standing below on leaf (facing away in photograph). Female's dorsal carapace faces male. Male viewed side on (his dorsal body turned to left in photograph). Male's legs I contacting left side of female's cephalothorax. Photograph: R. Jackson.

Fig. 5.8. *Evarcha culicivora* male (facing right) mounting female (facing left) while buried within an inflorescence of *Lantana camara*. Photograph: R. Jackson.

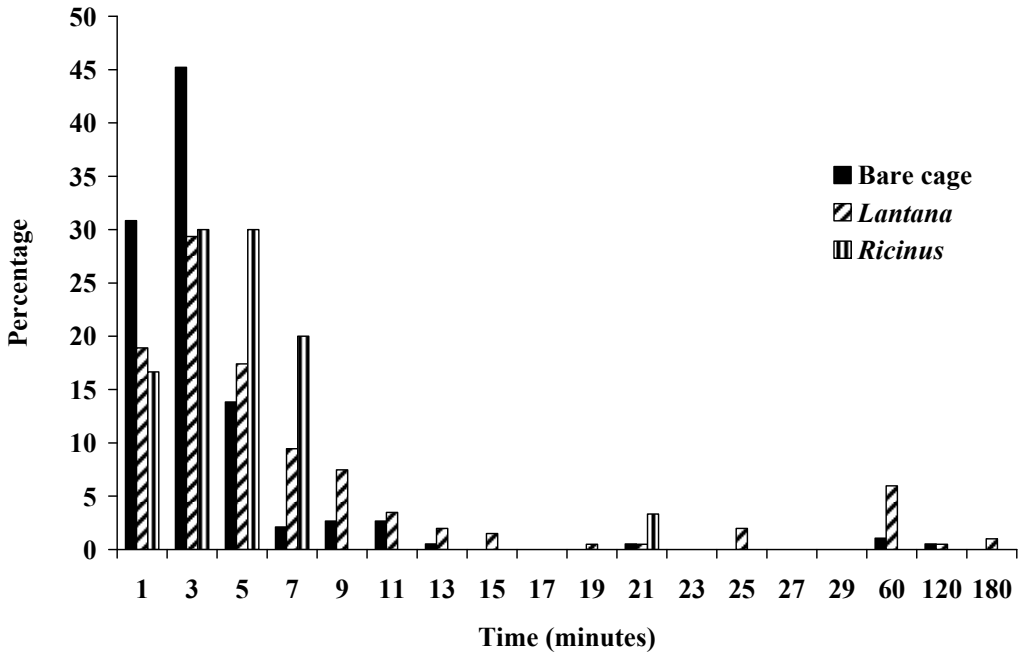

Fig. 5.9. Duration (min) of male-female interactions (Bare cage: Mean +/- *SD* = 4.81 +/- 14.35, *N* = 188; *Lantana*: Mean +/- *SD* = 10.81 +/- 23.24, *N* = 201; *Ricinus*: Mean +/- *SD* = 4.67 +/- 3.68, *N* = 30).

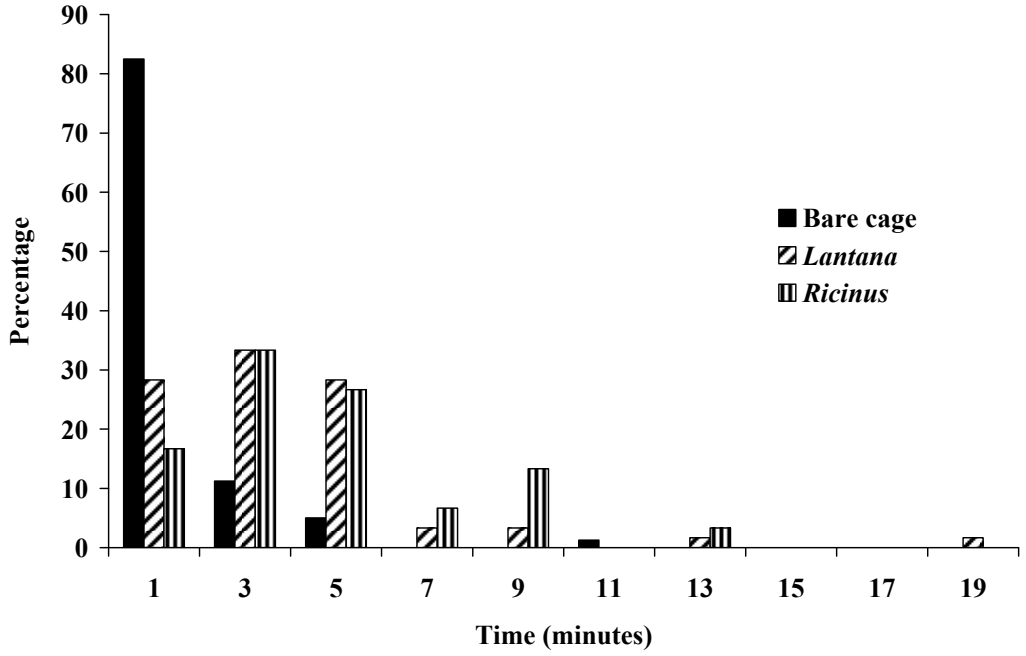

Fig. 5.10. Duration (min) of male-male interactions (Bare cage: mean +/- *SD* = 1.55 +/- 1.49, *N* = 80; *Lantana*: mean +/- *SD* = 3.77 +/- 3.08, *N* = 60; *Ricinus*: mean +/- *SD* = 4.60 +/- 2.94, *N* = 30).

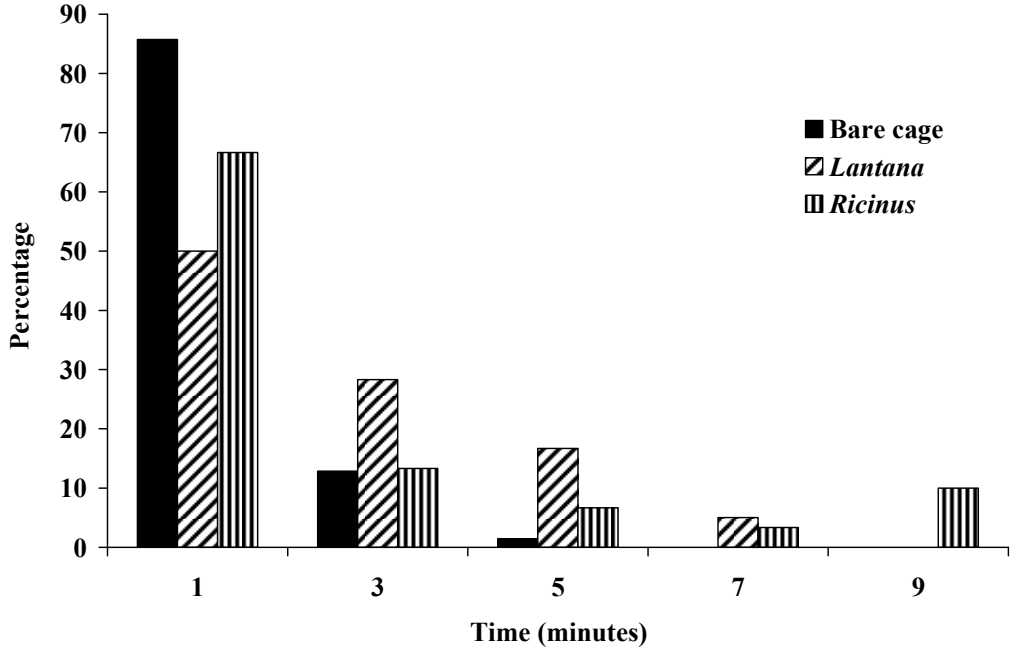

Fig. 5.11. Duration (min) of female-female interactions (Bare cage: mean +/- *SD* = 1.31 +/- 0.81, *N* = 70; *Lantana*: mean +/- *SD* = 2.53 +/-1.82, *N* = 60; *Ricinus*: mean +/- *SD* = 2.53 +/- 2.66, *N* = 30).

Chapter 6

Odour-mediated response to plants by *Evarcha culicivora*, a blood-feeding jumping spider from East Africa

In Chapter 5, I described how *Evarcha culicivora*'s interactions on *Lantana camara* and *Ricinus communis* are especially complex and variable. These two plant species appear to be an important part of *E. culicivora*'s biology, but at this stage the relationship *E. culicivora* has with these plants remains particularly elusive. As a first step in getting a better understanding of this relationship, in Chapter 6 I investigate whether *E. culicivora* can identify *L. camara* and *R. communis* by odour alone. In Chapters 2 and 3, I showed that *E. culicivora* uses olfaction, in sometimes surprising ways, for identifying and choosing potential mates. It can also use olfaction for identifying its preferred prey, blood-carrying mosquitoes (Jackson et al., 2005). However, whether *E. culicivora* can also use olfaction for identifying preferred plants has not been explored until now.

Lunch at Kisumu Airport, Kenya. Whole tilapia (fish) with some sukuma wiki (the green stuff, on the right)

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Odour-mediated response to plants by *Evarcha culicivora*, a blood-feeding jumping spider from East Africa

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Abstract *Evarcha culicivora* Wesolowska & Jackson, a salticid from the Lake Victoria region of East Africa, is known to associate with *Lantana camara* L. (family Verbenaceae) and *Ricinus communis* L. (family Euphorbiaceae), two plant species that are common in the same habitat. *E. culicivora* is an unusual salticid because, by choosing blood-carrying mosquitoes as preferred prey, it feeds indirectly on vertebrate blood, and *E. culicivora* apparently also feeds on nectar taken from *L. camara* and *R. communis*. The experimental findings reported here show that the odour of these two plants is salient to *E. culicivora*. A Y-shaped olfactometer was used in the experiments, with plant odour on one side and the other side a control (no odour). Juveniles, adult males and adult females chose the odour of *L. camara* and *R. communis* more often than the control.

Keywords nectar feeding; olfaction; Salticidae; spider-plant relationship

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INTRODUCTION

Jumping spiders (Araneae, Salticidae) are well known for their complex eyes (Land 1969a,b; Blest et al. 1990) and for having eyesight based on a level of spatial acuity exceeding that of all other animals in their size range (Harland & Jackson 2004). However, many salticids are also known to make considerable use of chemical cues (Pollard et al. 1987; Jackson & Pollard 1997; Jackson et al. 2002, 2005), *Evarcha culicivora* Wesolowska & Jackson being a striking example. This unusual salticid from the Lake Victoria region of East Africa is the only predator known to feed indirectly on vertebrate blood, achieving this by routinely choosing as preferred prey blood-carrying female mosquitoes (Wesolowska & Jackson 2003; Jackson et al. 2005; Nelson et al. 2005). *E. culicivora* can identify blood-carrying female mosquitoes with remarkable accuracy not only by sight alone but also by odour alone (Jackson et al. 2005).

Salticids are also known for having some of the most complex vision-based courtship routines in the animal kingdom (Jackson & Pollard 1997), with *E. culicivora*'s courtship behaviour being exceptionally complex even for a salticid (Cross et al. 2008) and departing in interesting ways from the salticid norm. The general pattern with salticids seems to be for males to place greater emphasis on displaying during courtship and for females to place greater emphasis on deciding whether to mate with the courting male. However, with *E. culicivora*, both sexes are active participants in courtship (Cross et al. 2008) and both sexes make distinctive mate-choice decisions (Cross et al. 2007). Moreover, *E. culicivora* is the only salticid for which we have experimental evidence that mate identification can be achieved when restricted to using odour cues alone (Cross & Jackson in press).

Yet another unusual characteristic of *E. culicivora* is that courtship may often take place with the male-female pair on one or the other of two particular plant species, *Lantana camara* L. (family Verbenaceae) and *Ricinus communis* L. (family Euphorbiaceae) (Cross et al. 2008) (Fig. 1). Behaviour patterns of

both sexes appeared exaggerated when they were on these plants (i.e., there was more variability during the performance of displays and there was generally more movement by the spiders) and the duration of interactions was longer (see Cross et al. 2008). Moreover, both sexes appeared reluctant to leave (especially when on *L. camara*), even when we prodded them aggressively with a fine paint brush (Cross et al. 2008). This was less evident when the spiders were on unrelated plants.

Lantana camara, native to tropical and subtropical America (Day et al. 2003), is an introduced noxious weed species (Ghisalberti 2000) in many parts of the world, including East Africa. Growing to 1–2 m in height, it has small aromatic flowers grouped together in inflorescences of red/pink, orange and yellow flowers (Schemske 1983; Parsons & Cuthbertson 2001). *R. communis*, commonly known as the castor oil plant, is native to tropical Africa (Cronk & Fuller 1995) and it can grow to about 3 m tall. It has small reddish green flowers and it also has extra-floral nectaries.

Currently the adaptive significance of *E. culicivora*'s affinity for these plant species is poorly understood, but a wide range of hunting spiders (i.e., spiders that do not build webs) have been documented supplementing their predatory diet by feeding on nectar (Pollard et al. 1995; Taylor & Foster 1996; Patt & Pfannenstiel 2008; Taylor & Pfannenstiel 2008), and nectar meals may sometimes be an important alternative food source when prey are scarce (Vogelei & Greissl 1989). Consistent with how nectar feeding appears especially common among salticids (Jackson et al. 2001), we have observed that juveniles, adult males and adult females of *E. culicivora* in the field sometimes press their chelicerae into *L. camara* flowers or into the extra-floral nectaries of *R. communis*, with these most likely being instances of the spider feeding on nectar. We also observed this when *E. culicivora* was given access to *L. camara* and *R. communis* in the laboratory (Fig. 1). Here we investigate whether, for *E. culicivora*, the odours of *L. camara* and *R. communis* are salient.

MATERIALS AND METHODS

Our field site and laboratory were at the Thomas Odhiambo Campus (Mbita Point, 0°25′S–0°30′S by 34°10′E–35°15′E, 1200 m above sea level, mean annual temperature of 27°C) of the International Centre of Insect Physiology and Ecology (ICIPE) in western Kenya. All laboratory work was carried out between 0800 h and 1300 h (laboratory photoperiod 12L:12D, lights on at 0700 h). Standard spider-laboratory procedures were as in numerous previous studies (see Jackson & Hallas 1986; Cross et al. 2008) and only essential details are provided here.

We tested males (body length 5 mm) and females (5 mm) of *E. culicivora* that had reached maturity (i.e., had undergone their final moult) 7–10 days earlier, had not mated and had not encountered any conspecific individuals since emerging from their egg sacs, as well as juveniles (i.e., immature individuals that had moulted 8–12 days before used, were 3 mm in body length, did not moult again in fewer than 10 days after used and, after moulting, were still immature). No spiders had been in contact with plants of any species before testing began, and no individual spider was tested more than once. The laboratory-rearing environment was "enriched" (spacious cages, mesh works of twigs within each cage), which has been shown to improve performance of salticids in experiments (Carducci & Jakob 2000), and all spiders were maintained on a diet of chironomids and blood-fed *Anopheles* females three times a week (see Jackson et al. 2005).

A Y-shaped olfactometer (Fig. 2) was used to assess *E. culicivora*'s response to plant odours. With a Matheson FM-1000 flow meter, airflow was adjusted to 1500 ml/min. There was no evidence that this airflow setting impaired locomotion or had any adverse effects on *E. culicivora*'s behaviour. Air was pushed by a pump from a tap through two separate flow meters into two chambers, a stimulus chamber and a control chamber. Each chamber was a glass cube made from 5 mm thick glass (inner dimensions, 70 × 70 × 70 mm), with a removable lid. There were two holes (diameter 20 mm) in the cube that were opposite each other and each was plugged with a rubber stopper. There was a hole in each stopper through which a glass tube (diameter 4 mm) passed. A nylon-netting screen over the stopper ensured that the test spider could not enter the chamber. New netting was used for each test. Air moved into and out of the stimulus chamber through the glass tubes to the stimulus arm, and independently from the control chamber to the control arm. Collectively, the two arms are referred to as the "choice arms". Air moved from the two choice arms into the "test arm" (i.e., the stem of the Y).

The stimulus chamber contained a cutting from a plant and the control chamber was empty. Cuttings always included flowers, leaves and stems (i.e., we were interested in seeing whether *E. culicivora*

Fig. 1 *Evarcha culicivora* on plants. Juvenile and adult male on *Ricinus communis*. Adult female on *Lantana camara*.

chooses plant odour, not just flower odour), and they came to half the height of the chamber (i.e., they did not rise above the level of the inflow and outflow holes in the stimulus chamber). Plant material was placed in the stimulus chamber 30 min before each test. This 30 min period allowed air to circulate evenly and ensured that air pressure was comparable throughout the olfactometer. For each test, whether the stimulus chamber was on the left or right side of the olfactometer was decided at random.

A test spider was confined to a holding chamber (Fig. 2) at the far end of the test arm for 2 min before testing began. A removable metal grill was fitted into a slit in the chamber roof, blocking access to the test arm from the holding chamber. The grill was lifted to start a test. Once the spider left the holding chamber, it was allowed 30 min to make a choice (definition: entered a choice arm and remained there for 30 s). Spiders usually walked about actively in the olfactometer and we recorded which of the two arms it chose. As a precaution against the potential effects of traces left by spiders that had been tested previously, the olfactometer was dismantled and cleaned with 80% ethanol and then with distilled water between tests.

For this study, all data were analysed using chi-square tests for goodness of fit (null hypothesis: probability of making one of the two choices same as probability of making other choice) (see Howell

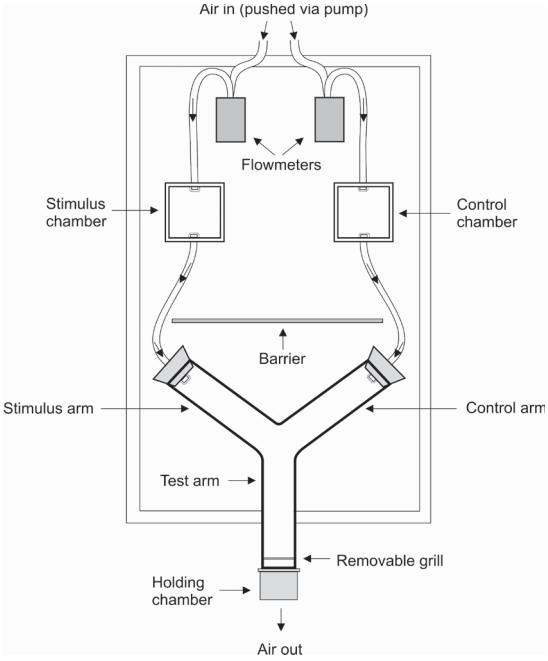

Fig. 2 Olfactometer (not drawn to scale). Arrows indicate direction of airflow. Holding chamber (location of test spider at start of test): length 25 mm, internal diameter 25 mm. Start of test: test spider in holding chamber; grill removed, giving access to test arm, control arm and stimulus arm. Dimensions of test arm, control arm and stimulus arm: length 90 mm, internal diameter 20 mm. Opaque barriers prevent test spider from seeing odour source.

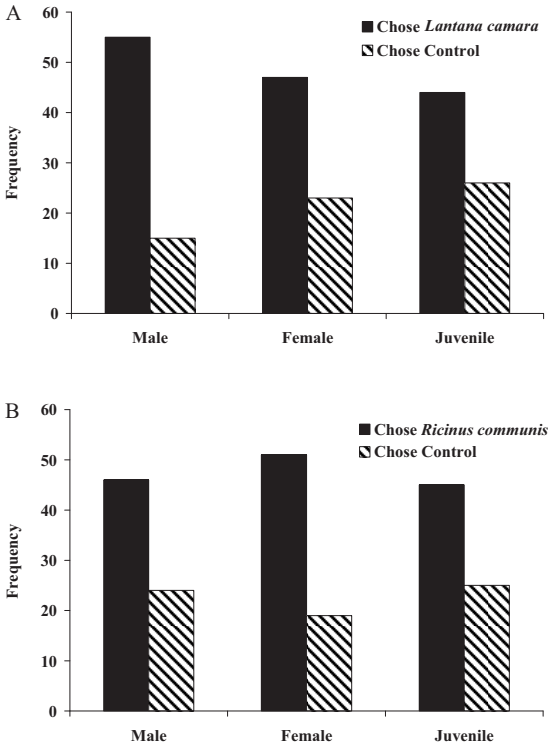

Fig. 3 Results from testing *Evarcha culicivora* males, females and juveniles in olfactometer showing odour of (**A**) *Lantana camara* and (**B**) *Ricinus communis* was chosen significantly more often than control (no odour).

2002). For data analysis, individuals that failed to choose were ignored. For each test, $N = 70$.

Voucher specimens of *E. culicivora* were deposited at the National Museums of Kenya (Nairobi), the Museum of Natural History (Wroclaw University, Poland) and the Florida State Collection of Arthropods (Gainesville, Florida).

RESULTS

Evarcha culicivora males ($\chi^2 = 22.86$, $P < 0.001$), females ($\chi^2 = 8.23$, $P = 0.004$) and juveniles ($\chi^2 = 4.63$, $P = 0.031$) chose *L. camara* odour significantly more often than the control (Fig. 3A), and males ($\chi^2 = 6.91$, $P = 0.009$), females ($\chi^2 = 14.63$, $P < 0.001$) and juveniles ($\chi^2 = 5.71$, $P = 0.017$) chose *R. communis* odour significantly more often than the control (Fig. 3B). For any given combination of spider sex-age class and plant species, the number of spiders that failed to choose was always less than 5%.

DISCUSSION

Our experimental results indicate that the odour of *L. camara* and *R. communis* is salient to the males and the females of *E. culicivora*. These results are an important first step towards understanding what appears to be an unusual spider-plant relationship. The adaptive significance of *E. culicivora*'s association with *L. camara* and *R. communis* is still poorly understood, but there are many examples in the literature of insects that associate with particular plant species, especially insects that may specialise at feeding on plant products, such as nectar and pollen, from particular plants (Chittka et al. 1999; Waser & Ollerton 2006; Díaz et al. 2007; Goulson et al. 2007; Brodmann et al. 2008).

Although there are fewer examples, some spiders associate with particular types of plants, namely pitcher plants (Cresswell 1993) and bromeliads (Romero & Vasconcellos-Neto 2004, 2005). Besides opportunities for nectar and pollen meals, associating with plants may reward spiders with opportunities to feed on insects that land on the plants (Whitney 2004). Plants bearing sticky glandular hairs may even function as insect traps, facilitating prey capture by the spiders that associate with these plants (Vasconcellos-Neto et al. 2007). Moreover, plants may benefit from the presence of spiders through increased seed production (Ruhren & Handel 1999; Whitney 2004).

For *E. culicivora*, nectar from *L. camara* and *R. communis* may have an important role as a food source. However, *E. culicivora*'s association with these plant species appears to differ from that of other spiders because of the unusual relevance these plants seem to have for adult *E. culicivora* in the context of courtship and finding mates. We are currently investigating this plant association in more detail. Preliminary results from experiments using plants that are related and unrelated to *L. camara* and *R. communis* suggest considerable specificity in *E. culicivora*'s plant preferences and there are also suggestions of surprising effects, including odour from *L. camara* and *R. communis* priming males and females of *E. culicivora* for encounters with potential mates.

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Chapter 7

Dancing to different odours: a case of spidernip?

Abstract

Evarcha culicivora, a jumping spider (Salticidae) from the Lake Victoria region of East Africa, is of particular interest because of how it makes use of olfaction when identifying potential mates, preferred prey and preferred plants. Here I consider instances in which the olfaction-based identification behaviour of *E. culicivora* may go beyond simply moving towards, or remaining in the vicinity of, an odour source. In the presence of these odours, males sometimes begin displaying in much the same way as during normal male-female interactions, only now there is no actual female visible as a target for the male's displaying. In preliminary experiments, displaying while exposed to these odours never happened in more than half the tests. Yet these experiments showed that, compared to the number of males that displayed in the control (no odour) or in the presence of the odour from *Heliotropium arborescens* (family Boraginaceae), there were significantly more males that displayed in the presence of odour from potential mates, prey (blood-carrying *Anopheles gambiae* and blood alone), and plants from the family Verbenaceae (*Lantana camara*, *Lantana montevidensis*, *Verbena* sp., *Aloysia citrodora*). These findings are discussed in the context of how *E. culicivora*'s mating strategy, predatory strategy and plant-use strategy overlap.

Introduction

Although jumping spiders (Araneae: Salticidae) are better known for having unique, complex eyes (Harland & Jackson, 2004; Land, 1969a,b), they are also one of the spider families for which we have the most experimental evidence of how chemosensory systems come into play in mating and predatory strategies (Huber, 2005; Jackson et al., 2002, 2005; Pollard et al., 1987). *Evarcha culicivora* has given us particularly striking examples, as this species can identify, by odour alone, potential mates (Cross & Jackson, in press; see Chapter 2), blood-carrying mosquitoes (Jackson et al., 2005) and even particular plant species (Cross & Jackson, 2009; see Chapter 6), as well as potential mates that have recently fed on preferred prey (Chapter 3).

Here I consider preliminary work that arose from incidental observations while carrying out olfactometer experiments for Chapters 2, 3 and 6. When *E. culicivora* males were alone in a Y maze or in a retention-test apparatus, with no other spider in sight, sometimes they began displays in much the same way as during normal courtship sequences in the presence of a female. This was not so startling when the odour was that of a conspecific female, but displays being elicited by dietary and plant odours seemed particularly mysterious. Inevitably, I thought about cats and catnip (see Palen & Goddard, 1966), but the catnip literature could not simply explain why these *E. culicivora* males seemed to be acting crazy. The objective in this chapter is to document this seemingly paradoxical behaviour and to take first steps toward understanding what is going on.

One thing that stood out was how displaying, instead of being a routine occurrence, happened only occasionally and unexpectedly, and one of the first missions was to find a better way for controlling when displaying would occur, making it happen more often and more predictably. I had little success on that

particular mission, as I never managed to persuade the spiders to display more than 40% of the time. However, I will present data from the methods that worked a little better than the rest.

Materials and Methods

Using standard salticid-laboratory procedures (see Cross et al. (2008) (Appendix 6), this work was carried out at the Thomas Odhiambo Campus of the International Centre of Insect Physiology and Ecology (ICIPE) (Mbita Point, western Kenya) and at the University of Canterbury (Christchurch, New Zealand) using cultures established from individuals collected at Mbita Point. All testing was carried out between 0800 h and 1300 h (laboratory photoperiod 12 light: 12 dark, lights on at 0700 h). For definitions of, and details about, the specific behaviour patterns I mention in this chapter, it may be useful to refer to Cross et al. (2008) (see Appendix 6).

Test spiders were adult males (virgins) of *E. culicivora* that were of standardised size (5 mm), had reached maturity 7–14 days before tested, and had no experience with any of the odour sources before use in experiments. No test spider was used more than once in the same experiment, and no odour source was used more than once. Spiders were fed 3–4 days before they were used in the experiments.

The odour sources used in experiments belonged to three different categories (Table 7.1). 'Spider' odour was the odour of potential mates (i.e., *E. culicivora* females) that had been maintained on a lake-fly (*Nilodorum brevibucca*, Chironomidae) diet. 'Dietary' odour was the odour of blood-carrying female mosquitoes (*Anopheles gambiae*; given human blood 4–5 h before being used), as well as the odour of blood alone (expired human blood, from a blood bank in Christchurch, that was not, and never

had been, inside a mosquito). 'Plant' odour was the odour of *Lantana camara* (Verbenaceae), as well as the odour of other plants from the family Verbenaceae (*Lantana montevidensis*, *Verbena* sp. and *Aloysia citrodora*). I also used *Heliotropium arborescens*, an unrelated plant (from the family Boraginaceae). There were also control tests (no experimental odour source present).

During testing, air was pushed through one of two stimulus chambers and then into a test chamber (Fig. 7.1). Airflow was always adjusted to 1500 ml/min (Matheson FM-1000 airflow regulator) and there was no evidence that this airflow setting impaired locomotion or had any adverse effects on *E. culicivora*'s behaviour. The stimulus chambers were either cylindrical (made of 1-mm thick glass; length 90 mm, inner diameter 20 mm) or were cubical (made of 5-mm thick glass; inner dimensions, 70 × 70 × 70 mm). Cylindrical chambers were used only when the odour source was a spider. In each cubical chamber, there were two holes. These holes were opposite each other (diameter 20 mm; centred on side of chamber) and each of these holes, as well as each end of the cylindrical chamber, was plugged with a rubber stopper. There was a hole in each stopper through which a glass tube (diameter 4 mm) passed and air moved into and out of the chambers through these glass tubes. Silicone tubes that connected to the glass tubes bridged airflow between components of the apparatus. The ends of the silicone tubes were covered with nylon netting to prevent the test spider from getting access to the odour sources. Test chambers were also cubical, but they had three holes (two holes on opposite sides and one hole in the lid). The hole in the lid was used for introducing the test spider, and was otherwise plugged with a silicone tube covered with netting for air outflow.

Odour sources were put in the stimulus chambers 30 min before testing began. For spider odour, there were 10 stimulus chambers, five on one side of the test

chamber and five on the other side of the test chamber. Each stimulus chamber held one *E. culicivora* female (5 mm in body length). For other tests, there were only two stimulus chambers, one on each side of the test chamber. For dietary odour, 20 blood-carrying mosquitoes, or 1 ml of blood, were put in each stimulus chamber. Plant material used as odour sources filled each stimulus chamber to half its height (i.e., it did not rise above the level of the inflow and outflow holes of the chambers). I took cuttings of flowers from potted plants, and any arthropods visible on the material were removed 60–90 min before the cuttings were put in the stimulus chambers. In control tests, there were two stimulus chambers and they were left empty.

The test chamber was surrounded by a 'fence' (wooden barrier, 200 mm × 120 mm) that was painted white, and this fence hid any odour sources from the test spider's view (stimulus chambers were positioned outside of this fence). There was a hole in two of the sides of the fence through which the silicone tubes passed (diameter of holes slightly bigger than diameter of silicone tube). The holes in the fence were positioned at the same height as the holes in the test and stimulus chambers.

Before the test began, the test spider was in a vial for 5 min. The netting-covered silicone tube in the lid of the test chamber was removed, and the spider was gently nudged into the chamber using a fine paint brush. Once the test spider was inside the chamber, testing ended 30 s after he finished displaying for the first time (see below). If he did not display, testing ended 30 min after he entered the chamber. Between tests, the chambers were dismantled and cleaned with 80% ethanol, followed by distilled water, and then dried. For access to the interior when cleaning, there was a removable top on each cubical chamber.

Data were analysed using chi-square tests of independence, Bonferroni adjustments being applied whenever there was repeated testing of the same data sets (see Howell, 2002).

Results

Observed behaviour

During courtship, males typically posture with legs erect or hunched, dance, twitch their abdomens and vigorously step with their palps (i.e., they moved the two palps up and down in an alternating fashion, as if stepping in the air) in front of a female (for definitions of behaviour patterns, see Cross et al., 2008; Appendix 6), and these are the displays I observed males sometimes performing in the test chamber. There were also instances of males freezing when they were in chambers with odour present, after which they began twitching their palps (i.e., jerking their palps up and down, amplitude 0.5–1 mm) and then gradually switching to palp stepping and also moving their palps faster. As their palps became more active, males usually started moving actively around the test chamber and, when displays occurred, it was usually leg posturing and abdomen twitching during the pauses between steps.

Rate of displaying

When tested with odours the number of males that displayed was always fewer than the number that did not display (Table 7.1). Males never displayed in control tests, and only one male (out of 46) displayed in the presence of odour from *H. arborescens*. The number of males that displayed in tests with *H. arborescens* was not significantly different from the number that displayed in control tests ($\chi^2 = 1.05$, $p = 0.304$).

Significantly more males displayed in the presence of the odour of *E. culicivora* females than in control tests ($\chi^2 = 19.86$, $p<0.001$) (Table 7.1).

The number of males that displayed in the presence of blood-carrying mosquitoes was not significantly different from the number that displayed in the presence of blood alone ($\chi^2 = 1.44$, $p = 0.231$). Significantly more males displayed in both of these tests than in the control (blood-carrying mosquitoes: $\chi^2 = 9.44$, $p = 0.004$; blood only: $\chi^2 = 20.12$, $p<0.001$) (Table 7.1).

The number of males that displayed in the presence of the odour of any one of the plant species from the family Verbenaceae was not significantly different from the number that displayed in the presence of odour of any other species from the same family (*L. camara* with *L. montevidensis*: $\chi^2 = 0.05$, $p = 0.818$; *L. camara* with *Verbena* sp.: $\chi^2 = 0.48$, $p = 0.486$; *L. camara* with *A. citrodora*: $\chi^2 = 0.21$, $p = 0.645$; *L. montevidensis* with *Verbena* sp.: $\chi^2 = 0.98$, $p = 0.322$; *L. montevidensis* with *A. citrodora*: $\chi^2 = 0.06$, $p = 0.814$; *Verbena* sp. with *A. citrodora*: $\chi^2 = 1.65$, $p = 0.199$). However, the number of males that displayed when presented with the odour of each of the species from the family Verbenaceae was significantly more than the number that displayed when presented with the odour of *H. arborescens* (*L. camara*: $\chi^2 = 11.38$, $p = 0.001$; *L. montevidensis*: $\chi^2 = 10.30$, $p = 0.003$; *Verbena* sp.: $\chi^2 = 17.70$, $p<0.001$; *A. citrodora*: $\chi^2 = 9.27$, $p = 0.005$) and the number of males that displayed in control tests (*L. camara*: $\chi^2 = 15.79$, $p<0.001$; *L. montevidensis*: $\chi^2 = 14.27$, $p<0.001$; *Verbena* sp.: $\chi^2 = 22.25$, $p<0.001$; *A. citrodora*: $\chi^2 = 12.91$, $p<0.001$) (Table 7.1).

The number of males that displayed in the presence of *E. culicivora* females was not significantly different from the number that displayed in the presence of blood-carrying mosquitoes ($\chi^2 = 1.39$, $p = 0.238$), blood alone ($\chi^2 = 0.04$, $p = 0.845$), *L.*

camara ($\chi^2 = 0.22$, $p = 0.635$), *L. montevidensis* ($\chi^2 = 0.52$, $p = 0.472$), *Verbena* sp. ($\chi^2 = 0.03$, $p = 0.873$) or *A. citrodora* ($\chi^2 = 0.93$, $p = 0.335$) (Table 7.1).

Discussion

The basic finding from this study is that sometimes odour alone seems to be enough to trigger the vision-based display behaviour that *E. culicivora* males normally adopt when interacting with potential mates. They will display in an almost featureless test chamber with no other spider present, with the odour that suffices not only being the odour of conspecific females but also the odour of blood-carrying mosquitoes, blood all by itself, or even plants.

If, in the presence of female odour, the male had consistently directed his displays at any particular object, it would have been tempting to suggest that female odour primed him for finding a female and that he simply mistook this object for a female. However, not only were no actual females in view in the experimental apparatus, but there was also nothing else present that would seem even remotely to resemble a conspecific female. Nor did the male usually maintain any particular orientation to any of the few objects that were in view (e.g., stoppers) while displaying in the chamber. It seems more accurate to envisage female odour as a trigger for the male to broadcast displays, without any particular target being required. The male and the female of this species both take an active role in courtship (Cross et al., 2008) and perhaps the male's displaying helps him locate an as-yet not-seen female by provoking her into displaying in response to his display. An alternative, but not mutually exclusive, hypothesis is that displaying functions as pre-emptive defence against cannibalistic attacks by the female. These and other hypotheses should be tested in future research.

On the other hand, it is more of a challenge to identify hypotheses that might be relevant when it comes to dietary and plant odour eliciting courtship display. A mosquito or a plant is not a predator to be deterred by pre-emptive display and males do not mate with mosquitoes or plants. That males sometimes display when these are detected is paradoxical. Or is it?.

Considering the male's perspective, there actually are reasons to envisage the odour of blood-fed mosquitoes, and maybe even blood all by itself, as being relevant in the context of mating. The findings in Chapter 3 showed that, by feeding on blood-carrying mosquitoes, males and females became more attractive to the opposite sex. If blood is perfume for *E. culicivora*, then what is relevant from the male's perspective might be that where there is perfume there might also be a conspecific female.

Understanding the role of plants in *E. culicivora*'s biology has been an especially elusive goal, but there are hints that certain plants, *Lantana camara* and *Ricinus communis*, are somehow relevant to this spider's mating strategy (Cross & Jackson, 2009; Chapter 5 & 6). When doing previous olfactometer work with plants, I noticed that it was *L. camara* odour in particular that triggered courtship display. However, *E. culicivora*'s relationship with *L. camara* still remains a mystery. Although now very abundant in *E. culicivora*'s natural habitat, *L. camara* is an introduced weed in East Africa (Ghisalberti, 2000). There are native species from the same family, Verbenaceae, in East Africa, but they appear to be generally scarce in comparison with *L. camara*. However, I found that *E. culicivora* also displays when presented with odour from some other species from the family Verbenaceae, even though these species are not native to Africa and do not grow wild in *E. culicivora*'s habitat. This suggests that plants from the family Verbenaceae tend to share chemical characteristics that elicit *E. culicivora*'s display behaviour.

How readily *R. communis* odour elicits *E. culicivora*'s display behaviour is currently uncertain. Incidental to other work, we know that males sometimes display in the olfactometer when this plant's odour is present, but the experiments I carried out in this chapter using *L. camara* have not yet been carried out using *R. communis*.

If *L. camara* is a common meeting site for finding potential mates, then it may be understandable that the odour of this plant alone sometimes suffices to elicit courting, as the plant odour could be associated with the possibility of a female being in the vicinity. This seems likely to be a helpful strategy for finding females in such a complex environment. However, in future research, we should also investigate whether odour from *L. camara* is used by *E. culicivora* as a perfume. There is evidence that some insects use plant volatiles as perfume (e.g., Lunau, 1992), but this has not been documented for a spider. Blood-derived perfume is acquired by eating blood-carrying mosquitoes and perhaps *E. culicivora* acquires *L. camara* perfume when feeding on the plant's nectar. Another possibility is that, when *E. culicivora* is on *L. camara*, it picks up these compounds as perfume by absorbing them into its cuticle.

Yet I can not help but also wonder if *L. camara* is for *E. culicivora* something like catnip (*Nepeta cataria*) on cats. Sometimes I was tempted to say *E. culicivora* on *L. camara* was in a drug-like state, and similar interpretations have been put on a cat's behaviour around catnip. In the presence of this aromatic herb (Baranauskiene et al., 2003), cats rub against the plant material, roll around in it and generally act like they are in oestrous (Palen & Goddard, 1966), as though the catnip-intoxicated cat is hallucinating (Grognet, 1990). That catnip has striking effects on cat behaviour is well known, based on a wealth of anecdotal information, but I was surprised when I discovered how little is actually known about precisely how and why catnip makes

cats do these crazy things. *L. camara* sometimes seems to be *E. culicivora*'s version of catnip. Now, besides being frustrated by how little we actually understand about the cat's weakness for catnip, we seem to have a similar arachnid puzzle to solve.

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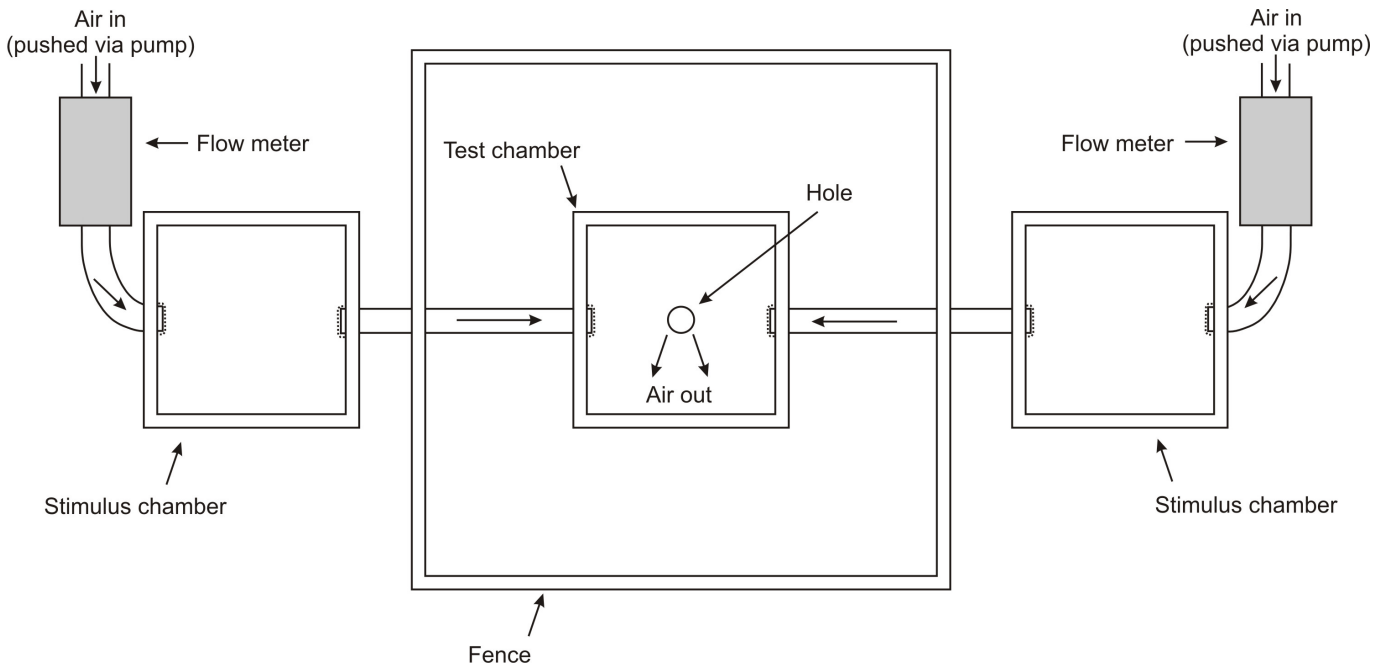

Fig. 7.1. Experimental apparatus (not drawn to scale) for presenting *Evarcha culicivora* males with different odour sources. Arrows indicate direction of airflow (exiting out of hole in test chamber). Male in test chamber, with odour sources (in stimulus chambers) hidden behind fence.

Table 7.1. Results of tests using different odour sources.

Type of odour	Odour source	N	Male displayed	Male did not display
Spider	*Evarcha culicivora* females	16	6 (37.5%)	10 (62.5%)
Dietary	Blood-carrying *Anopheles gambiae* females	16	3 (18.75%)	13 (81.25%)
	Blood only	46	16 (34.78%)	30 (65.22%)
Plant	*Lantana camara* (Verbenaceae)	20	6 (30%)	14 (70%)
	Lantana montevidensis (Verbenaceae)	26	7 (26.92%)	19 (73.08%)
	Verbena sp. (Verbenaceae)	25	10 (40%)	15 (60%)
	Aloysia citrodora (Verbenaceae)	33	8 (24.24%)	25 (75.76%)
	Heliotropium arborescens (Boraginaceae)	46	1 (2.17%)	45 (97.83%)
Control	No odour source	48	0 (0%)	48 (100%)

Chapter 8

How cross-modality effects during intraspecific interactions of jumping spiders differ depending on whether a female-choice or mutual-choice mating system is adopted

In Chapters 2, 3, 6 and 7, I showed that *Evarcha culicivora*'s use of olfaction is especially pronounced. Olfaction plays a role for this salticid in identifying and choosing potential mates, as well as in identifying preferred plants. In Chapter 7, I showed that *E. culicivora* can even use olfaction in sometimes surprising ways. Here, in Chapter 8, I extend some of this previous work by investigating whether *E. culicivora* uses olfactory cues for making decisions about fighting with a potential rival (a same-sex conspecific). Mutual mate choice is pronounced in this species (Cross et al., 2007a; 2008) and, in this chapter, I investigate whether both sexes of *E. culicivora* escalate conflict with a rival more when they are presented with the odour of a potential mate (an opposite-sex conspecific) rather than an unrelated salticid of the opposite sex (an opposite-sex heterospecific). These results are compared with the results for three other salticid species without a mutual mate choice system, where males are generally more active in courtship and where females generally choose males as mates.

Orphaned elephants being cared for in the Sheldrick Wildlife Trust, Nairobi, Kenya

Pages 123-129 of thesis.

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How cross-modality effects during intraspecific interactions of jumping spiders differ depending on whether a female-choice or mutual-choice mating system is adopted

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Abstract

An important prediction from game theory is that the value of a resource influences the level to which conflict escalates. Here we use jumping spiders (Salticidae) to consider this prediction in the context of species adopting different mating systems (‘female mate-choice’ and ‘mutual mate-choice’). Our experiments are designed for determining whether the odour of conspecific females, more than the odour of heterospecific females, primes males to escalate conflict with a potential same-sex rival and also whether the odour of conspecific males, more than the odour of heterospecific males, primes females to escalate conflict with a potential same-sex rival. Four species were studied: *Evarcha culicivora*, a species in which mutual mate-

choice is pronounced, and *Portia fimbriata*, *Portia africana*, and *Jacksonoides queenslandicus*, more conventional salticids in which female mate-choice and male–male competition appear to be dominant. Our hypothesis is that, for all four species, there is strong competition between males for access to females and that, for *E. culicivora*, but not for the other three species, there is also strong competition between females for access to males. Our findings are consistent with this hypothesis, as we show that, although the odour of conspecific females primes escalation of vision-based male–male conflict for all four species, *E. culicivora* is the only species for which there is evidence of odour from conspecific males priming the escalation of female–female conflict.

Chapter 9

Cross-modality priming of visual and olfactory selective attention by a spider that feeds indirectly on vertebrate blood

In this thesis so far, I have focussed on how *Evarcha culicivora* uses olfaction in the context of its mate-choice system (Chapters 2, 3, 7 and 8), as well as in the context of its unusual relationship with two plant species, *Lantana camara* and *Ricinus communis* (Chapter 6). However, until now, I have paid little attention to how *E. culicivora* might use olfaction (or vision, for that matter) for finding its preferred prey, blood-carrying mosquitoes. Previous work (Jackson et al., 2005) had shown that *E. culicivora* can use visual and olfactory cues for identifying this prey, but here, in Chapter 9, I consider how *E. culicivora* might use both vision and olfaction when selectively attending to this prey. More specifically, in this chapter, I investigate cross-modality priming and whether the odour of blood-carrying mosquitoes primes *E. culicivora* for seeing this prey. However, I also investigate something that is not normally considered, whether cross-modality priming might also work in the other direction, with the appearance of blood-carrying mosquitoes priming *E. culicivora* for finding the odour of this prey. The work in this chapter has been accepted for publication in *Journal of Experimental Biology*.

Zebra in Nairobi National Park, Kenya

Cross-modality priming of visual and olfactory selective attention by a spider that feeds indirectly on vertebrate blood

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Short title: Cross-modality priming by a salticid

Summary

Evarcha culicivora, a jumping spider from East Africa, specialises at feeding indirectly on vertebrate blood by choosing blood-carrying mosquitoes as preferred prey. Previous studies have shown that this predator can identify its preferred prey by sight alone and also by odour alone. Here we investigate how vision and olfaction work together. Our findings show that, for *E. culicivora*, cross-modality priming in the context of preying on blood-carrying mosquitoes works in two directions. However, we found no evidence of priming in the context of predation on less preferred prey (midges). When the spider's task was, by sight alone, to find a cryptic lure, it found mosquitoes significantly more often when the odour of mosquitoes was present than when this odour was not present. When the spider's task was to find masked odour, it found mosquitoes significantly more often after previously seeing mosquitoes than when it had not previously seen mosquitoes. When the spider's task was to find conspicuous lures or unmasked odour, the identity of the priming stimulus appeared to be irrelevant. Results were similar regardless of the spider's prior experience with prey and suggest that *E. culicivora* has an innate inclination to adopt vision-based search images specifically for mosquitoes when primed by mosquito odour and to adopt olfaction-based search images specifically when primed by seeing mosquitoes.

Key words: Salticidae; cognition; olfaction; predation; search images; vision

Introduction

Research on attention, like most cognition research, has mainly been human based (e.g., Pashler, 1998) but, independent of this tradition in psychology, biologists who study the behaviour of non-human animals have also laboured over the topic of attention, but largely by another name, 'search images'. This is a term that can be traced back to von Uexküll (1934) (see Bond, 2007) but is now most often associated with Tinbergen and the hypothesis he used for explaining his field-based data on insectivorous birds (Tinbergen, 1960).

Tinbergen (1960) envisaged search images as perceptual changes, the idea being that the predator, after discovering a particular type of prey, 'gets an eye for' or 'learns to see' this particular type of prey. In other words, having previous experience with a particular type of prey might prime a predator to become selectively attentive to specific features of this particular prey. This is the context in which the term 'search images' has been used in the more critical research following on from Tinbergen's classic paper (see Blough, 1991; Bond and Kamil, 2002; Dawkins 1971; Langley, 1996).

However, Tinbergen's search-image hypothesis has also been the source of considerable confusion (see Guilford and Dawkins, 1987), as researchers sometimes blur the distinction between selective attention and preference. Intuitively, a dietary 'preference' refers to what an animal would like to eat (i.e., something that is expressed by choice behaviour). Search images, on the other hand, are shifts in selective attention (Cross and Jackson, 2006; Shettleworth, 1998). A critical criterion for making this distinction is to compare experimental outcomes from trials in which prey is difficult to detect ("cryptic") with experimental outcomes from trials in which prey is easily detected ("conspicuous"). We expect selective attention to matter especially when prey is cryptic. When prey is conspicuous, we predict that the influence of selective attention will not be so emphatic and that the animal's preferences will instead be most evident.

Jumping spiders (Salticidae) are particularly suitable subjects for research concerned with vision-based prey identification because they have unique, complex eyes and vision based on a level of spatial acuity that is unrivalled by other animals in their size range (Harland and Jackson, 2004; Land, 1969). Salticids can be tested with immobile lures instead of living prey (Jackson and Tarsitano, 1993), which means we can

ascertain whether these predators have found potential prey in the absence of movement cues and without the actions of the prey individual confounding interpretation of experimental outcome. However, besides having exceptional eyesight, many salticids are known to make considerable use of chemical cues (Jackson and Pollard, 1996; Jackson and Pollard, 1997), with this suggesting that salticids may also be especially suitable subjects for research on cross-modality priming (i.e., research on the mechanisms by which information from one sensory modality causes attentional changes in another modality; see Calvert et al., 2004; Spence and Driver, 2004).

Here we consider the role of selective attention in the predatory strategy of *Evarcha culicivora* Wesolowska and Jackson, a salticid from the Lake Victoria region of East Africa. This salticid is unusual because it specialises at feeding on vertebrate blood, gaining access to blood indirectly by choosing as preferred prey blood-carrying mosquitoes (Jackson et al., 2005). For *E. culicivora*, satisfying a highly precise predatory preference may be particularly challenging. Mosquitoes, although plentiful in its habitat, are vastly outnumbered by other mosquito-size dipterans in this habitat, with non-biting midges, known locally as 'lake flies', from the families Chaoboridae and Chironomidae (Okedi, 1992) being especially common. Although *E. culicivora* eats lake flies as well as mosquitoes, the majority of its prey in nature is blood-carrying mosquitoes (Wesolowska and Jackson, 2003).

Knowing that *E. culicivora* can identify its unusual prey by sight alone and by odour alone (Jackson et al., 2005), our objective is to consider how vision and olfaction work together. Our hypothesis is that *E. culicivora* relies strongly on cross-modality priming of selective attention, with a stimulus in one sensory modality (vision or olfaction) triggering an innate search image in another modality (olfaction or vision). This departs from the tradition in the search-image literature of emphasising same-modality priming (i.e., instances of a stimulus in one sensory modality triggering selective attention in the same modality), where the sensory modality considered is usually vision. Another tradition in the search-image literature has been to base experiments on repeatedly exposing a predator to a particular type of prey, with an underlying hypothesis being that search images are acquired by perceptual learning. However, our hypothesis is that *E. culicivora* uses a system based on innate triggering of

selective attention (i.e., we predict that, for the predator, prior experience with the priming cue is unnecessary). As another departure from tradition, our hypothesis is that, for *E. culicivora*, cross-modality priming works in two directions (i.e., we propose that odour primes selective visual attention, and vision primes selective olfactory attention). We also propose that *E. culicivora* is predisposed to cross-modality priming effects in the specific context of encounters with its preferred prey (i.e., blood-carrying mosquitoes).

Materials and Methods

General

Our field site and laboratory were at the Thomas Odhiambo Campus of the International Centre of Insect Physiology and Ecology (Mbita Point) in western Kenya. Standard spider-laboratory procedures were adopted (Cross et al., 2008; Jackson and Hallas, 1986) and all trials were carried out between 0800 h and 1300 h (laboratory photoperiod 12L:12D, lights on at 0700 h).

We adopted some shorter terms for lures, odour and prey. "Mosquitoes" were always blood-carrying females of *Anopheles gambiae ss* (Culicidae). "Lake flies" were always *Nilodorum brevibucca* (Chironomidae). All spiders were fed to satiation three times a week on one of three diet regimes: mosquito diet, lake-fly diet or mixed diet (i.e., a diet of lake flies and mosquitoes). The spiders were always adult females of *E. culicivora* (virgin, matured 2–3 weeks before used in trials) and no individual spider was used more than once. We decided to use females instead of males because female salticids may generally be, compared with males, more strongly motivated to feed (Givens, 1978; Jackson and Pollard, 1997). As in an earlier study (Jackson et al., 2005), a short pre-trial fast (7 days) was adopted, the rationale for this being to ensure that the test spiders would be motivated to feed during the trials and to standardise the hunger level of test spiders. The mosquitoes used for feeding *E. culicivora*, for making lures and for odour sources in experiments had been given human blood 4–5 h before being used. Lake flies were collected from the field immediately before use.

Insects used for making lures were first immobilised with CO_2 and then placed in 80% ethanol. The next day, each insect was mounted in a life-like posture on the centre

of a disc-shaped piece of cork. For preservation, the lure and the cork were then sprayed with a transparent plastic adhesive.

Rationale

In previous research (Jackson et al., 2005), when a wide range of prey types were used in prey-choice experiments, *E. culicivora* consistently chose blood-carrying mosquitoes more often than other prey, and there was no suggestion of variation in how *E. culicivora* responded to the other prey. On this basis, we decided to standardise our priming experiments by using only mosquitoes and lake flies as prey.

There were two experimental designs (Fig. 9.1), one where *E. culicivora* was presented with the task of finding prey (a lure) by sight while being primed with prey odour (Experiment 1) and one where *E. culicivora* was presented with the task of finding prey by olfaction after having been primed by seeing prey (Experiment 2). The rationale for having two different experimental designs was to determine whether, for *E. culicivora*, cross-modality priming goes in both directions. Features common to both experiments will be described first, followed by details specific to each of the two experiments.

For distinguishing between effects of selective attention and effects of preference, there were two trial types, 'cryptic' and 'conspicuous', in each experiment. In the cryptic trials of Experiment 1, *E. culicivora* was presented with the task of finding a lure (Fig. 9.1A) that was behind nylon netting and accompanied by "distractors" (i.e., cork discs on which no lure was mounted). In the cryptic trials of Experiment 2, *E. culicivora* was presented with the task of finding prey odour that was accompanied by a masking odour (i.e., there was a potentially distracting odour in the 'cryptic' (i.e., 'masked') trials (Fig. 9.1B). For the masking odour, we used *Lantana camara*, a highly aromatic plant that is common in *E. culicivora*'s habitat. *E. culicivora* associates with this plant species (Cross et al., 2008) and is attracted to its odour (Cross and Jackson, 2009). The masking-odour source was put in chambers ("masking chambers") positioned in front of a control chamber (empty) and in front of a stimulus chamber that contained prey. We also included an extra chamber ('transition chamber') through which *E. culicivora* had to pass before getting close to an experimental odour source. The rationale for using the

transition chamber was to make the task of finding the masked prey more difficult for *E. culicivora*.

For both experiments, we also had other trials (conspicuous and unmasked) which were like the cryptic and masked trials except for the absence of the features intended to make prey difficult to find (i.e., in Experiment 1 (Fig. 9.1A), there was no netting and no distractors and, in Experiment 2 (Fig. 9.1C), there was no masking odour and no transition chamber).

General experimental methods

In both experiments, there was a 'stimulus chamber'. The stimulus chamber contained prey (either 10 mosquitoes or 10 lake flies) or, in Experiment 1, it was sometimes empty ('control'). In each trial in Experiment 2, there was always a stimulus chamber (contained prey) and a 'control chamber' (empty) and a 'priming chamber' (i.e., a chamber used for allowing *E. culicivora* to see a particular prey type before given an opportunity to locate prey odour). In masked trials of Experiment 2, there were also two masking chambers and a transition chamber.

Each chamber had two holes opposite each other. In both experiments, air moved into and out of stimulus, control and masking chambers through glass tubes (diameter 4 mm) inserted into rubber stoppers that plugged the holes. Airflow between components of the apparatus was bridged by silicone tubes that were connected to the glass tubes.

A pump coupled to a Matheson FM-1000 flow meter was used for pushing air through the apparatus. For permeating an arena with odour, the airflow system for Experiment 1 was similar to that used in a recent study (Cross et al., 2007). For Experiment 2, we modified a Y-shaped olfactometer used in earlier research on prey-choice decisions (Jackson et al., 2005). Airflow was set at 1200 ml/min in Experiment 1 and at 1500 ml/min in Experiment 2. There was no evidence that either of these airflow settings impaired locomotion or had any adverse effects on the test spider. Via a silicone tube, air went successively into one chamber (Experiment 1) or into more than one chamber (Experiment 2; see below) and then, via another silicone tube, either into an arena (Experiment 1) or into a Y maze (Experiment 2). The silicone tubes connecting the chambers to the testing apparatus were covered with nylon netting on the end facing into

the apparatus, blocking the spider's access to the chambers. Prey were put in the stimulus chambers (Experiments 1 and 2) and cuttings from *L. camara* (stems, leaves and flowers) were put in the lower half of each masking chamber (sufficient plant material added to not rise above level of inflow and outflow hole of chamber; Experiment 2 only) 30 min before trials began. The 30-min period allowed time for air to circulate evenly and ensured that air pressure was comparable throughout the apparatus. The plant material was collected from the field 60–90 min before put in the masking chamber (any visible arthropods on the material removed).

For both experiments, the entire apparatus was lit with a 200-W incandescent lamp that was positioned 400 mm overhead (additional ambient lighting from overhead fluorescent lamps). Between trials, the apparatus was dismantled and cleaned with 80% ethanol, followed by distilled water and then dried.

For trials with cryptic mosquito lures (Experiment 1) and for trials with masked mosquito odour (Experiment 2), we used test spiders that had been on each of three different diets (mosquitoes only, lake flies only and mixed). In all other trials, test spiders were on the mixed diet only.

Data for both experiments were analysed using chi-square tests of independence, Bonferroni adjustments being applied whenever the same data sets were analyzed more than once (see Howell, 2002). For both experiments, the relevant data were the number of spiders that found the lure or the odour. Data on latency, not being especially informative for the experimental designs we used, will not be considered here. For experiment 1, *N* for all conditions was 150 (i.e., 2400 individual spiders were tested). For experiment 2, unless stated otherwise, *N* for all conditions was 180 (*N* differed for spiders on mosquito diet and spiders on lake-fly diet (see Fig. 9.3B); 1781 individual spiders were tested in Experiment 2).

Experiment 1: Olfactory priming of visual selective attention

The testing apparatus (Fig. 9.1A) was a glass arena with four glass vials that fitted into holes on each of the four sides of the arena. A wooden wall surrounding the arena had a hole (diameter 12 mm) in the centre of each side through which the glass vials protruded (open end of each vial on inside of arena; other end closed).

On either side of each hole in the wall there was an indentation, and each indentation held a small Petri dish. In cryptic trials, each Petri dish covered five cork discs (attached with double-sided adhesive tape). One disc was in the centre of the indentation in the wall. The other four discs were spaced evenly around the rim of the dish, one of these discs being positioned where the dish rim was closest to the floor of the arena ('lower rim position'). The Petri dishes were also covered with nylon netting. In conspicuous trials, there was no nylon netting and there was also only one cork disc (always in the lower rim position) per Petri dish. For both treatments, there was a lure in only one of the Petri dishes (which of the dishes would have a lure decided at random for each trial). The disc on which the lure was mounted was always in the lower rim position and the lure was always facing into the arena.

The pump, flow meter and stimulus chamber were situated underneath the arena and wooden stand, with the stand shielding these parts of the apparatus from the test spider's view. The silicone tube connecting the stimulus chamber to the arena extended through a hole centred on the top of the wooden stand and then into the hole in the bottom of the arena (i.e., the two holes were aligned). The hole in the lid of the arena (for air outflow) was plugged with a silicone tube, with netting over the tube to prevent the spider from escaping. New netting was used for each trial.

The criterion adopted for recording that the test spider had 'found' the prey item was seeing the test spider enter the vial closest to the location of the lure and stay inside for at least 30 s. The rationale for the 30-s proviso was that, in preliminary trials, although *E. culicivora* sometimes entered a vial for a few seconds and then left, any individual that stayed in a vial for 30 s remained in this vial for at least 5 min and any that subsequently left this vial never entered and remained in another vial for as long as 30 s. We also adopted an alternative criterion: *E. culicivora* pressed its face against the side of the arena while facing directly towards the lure, but did not subsequently enter the vial. This criterion was never applicable in more than 10% of the recorded instances of finding prey for any treatment (Figs 9.2–3). Trials lasted until *E. culicivora* found the lure or, if *E. culicivora* did not find a lure, until 60 min elapsed.

Experiment 2: Visual priming of olfactory selective attention

How the apparatus was set up depended on whether the odour was masked or unmasked, but the basic components of the apparatus were the same for the two treatments.

There was a 'Y maze' made of glass, with the stem of the Y being the 'test arm', with one of the forks of the Y being the 'control arm' and with the other fork being the 'stimulus arm'. In masked trials (Fig. 9.1B), there was a stimulus chamber plus a masking chamber on one side of the Y and a control chamber plus a masking chamber on the other side. Air moved independently through the two chambers on the left side of the Y and through the two chambers on the right side of the Y. From the two arms of the Y, air then moved into the test arm and, from there, for the masked treatment only, through a corridor into a transition chamber and, from the transition chamber, through a holding chamber before exiting through a hole in the stopper. For the unmasked treatment (Fig. 9.1C), the path of air was the same except that there was no corridor, no transition chamber and no masking chambers.

For each trial, whether the stimulus chamber was on the left or the right side was decided at random. Before trials began, a test spider was put into a glass holding chamber that was inserted through the holes in the sides of a priming chamber (Fig. 9.1). There were 20 lake flies or 20 mosquitoes in the priming chamber. The holding chamber was positioned so that it protruded 5 mm out from each side of the priming chamber. There was a stopper in place at each end of the holding chamber, inserted deep enough so that it confined the test spider to the part of the tube inside the priming chamber where the insects were in view.

The test spider was kept for 10 min inside the holding chamber, after which the holding chamber was removed from the priming chamber. The end of the holding chamber closest to the location of the test spider was plugged with a stopper. For the unmasked treatment, the open end of the holding chamber was inserted through a hole in a stopper and this stopper was inserted into the open end of the test arm of the Y. The open end of the holding chamber was flush with the end of the stopper inside the Y. For masked trials, the open end of the holding chamber was inserted into one of the holes in the transition chamber (open end flush with inside of box).

The test spider was free to walk out of the holding chamber and enter the transition chamber (masked trials) or the test arm of the Y (unmasked trials). Once the test spider entered the transition chamber, it was free to enter a corridor and then the test arm (corridor fit in hole in a stopper which plugged the opening of the test arm).

Once in the test arm, the test spider was given 60 min to find the stimulus odour (i.e., to move into the stimulus arm and remain there for 30 s).

Results

Does the cryptic-conspicuous distinction matter?

Evidently the methods we used for making lures cryptic and for masking odour were effective. Regardless of the priming stimulus, spiders found conspicuous mosquito and lake-fly lures significantly more often than cryptic mosquito and lake-fly lures in Experiment 1 (Fig. 9.2A) and spiders found unmasked mosquito and lake-fly odour significantly more often than masked mosquito and lake-fly odour in Experiment 2 (Fig. 9.2B).

Does the priming stimulus matter when prey are conspicuous?

We found no evidence that the priming stimulus might matter when lures were conspicuous or when odour was unmasked. In Experiments 1 and 2, the number of spiders that found conspicuous or unmasked mosquitoes when primed with mosquitoes was not significantly different from the number of spiders that found conspicuous or unmasked mosquitoes when primed with lake flies (Fig. 9.2A,B) or, in Experiment 1, when there was no priming odour (control) (Fig. 9.2A). Likewise, the number of spiders that found conspicuous or unmasked lake flies when primed with lake flies was not significantly different from the number of spiders that found conspicuous or unmasked lake flies when primed with mosquitoes (Fig. 9.2A,B) or, in Experiment 1, when there was no priming odour (control) (Fig. 9.2A).

Does the priming stimulus matter when prey are cryptic?

In both experiments, it was evident that the priming stimulus mattered specifically when prey was hard to detect (cryptic lures or masked odour). In Experiments 1 and 2,

significantly more spiders found cryptic or masked mosquitoes when primed with mosquitoes than when primed with lake flies (Fig. 9.2A,B) or when there was no priming odour (control) (Fig. 9.2A). Few spiders found cryptic or masked lake flies, and the number of spiders that found cryptic or masked lake flies when primed with lake flies was not significantly different from the number of spiders that found cryptic or masked lake flies when primed with mosquitoes (Fig. 9.2A,B) or when there was no priming odour (control) (Fig. 9.2A).

Does the identity of the prey used as a lure (Experiment 1) or for prey odour (Experiment 2) matter?

On the whole, our findings corroborate the conclusion from earlier work (Jackson et al., 2005) that mosquitoes are *E. culicivora*'s preferred prey. A bias for mosquitoes was evident in conspicuous and unmasked trials. Whether primed with mosquitoes, primed with lake flies (Fig. 9.2A,B) or not primed (control) (Fig. 9.2A), significantly more spiders found mosquitoes than lake flies. A bias for mosquitoes was also evident in the cryptic and masked trials. Whether primed with mosquitoes (Fig. 9.2A,B) or not primed (control) (Fig. 9.2A), significantly more spiders found mosquitoes than lake flies. When primed with lake flies in Experiment 1, significantly more spiders found cryptic mosquitoes than lake flies (Fig. 9.2A), but a similar trend in Experiment 2 was not significant (Fig. 9.2B).

Does maintenance diet matter?

Cross-modality priming by cues from mosquitoes was evident regardless of the particular diet on which *E. culicivora* was maintained. In Experiment 1, the number of spiders that found cryptic mosquitoes in the presence of mosquito odour versus in the presence of lake-fly odour did not vary significantly depending on diet (Fig. 9.3A). In Experiment 2, the number of spiders that found masked mosquito odour after being primed by seeing mosquitoes versus lake flies did not vary significantly depending on diet (Fig. 9.3B).

Does the visual priming stimulus or identity of odour to be found affect E. culicivora*'s inclination to enter the Y maze (Experiment 2)?*

We wanted to determine whether being primed with a particular visual stimulus or being presented with a particular odour encouraged *E. culicivora* to enter the Y maze. For this, we compared the number of spiders that entered both the transition chamber and the Y maze with the number of spiders that entered the transition chamber but failed to enter the Y maze.

We found no evidence that the priming stimulus influenced the spider's inclination to enter the Y maze. When presented with masked mosquito odour, the number of spiders that entered the Y maze after seeing mosquitoes was not significantly different from the number of spiders that entered the Y maze after seeing lake flies. When presented with masked lake-fly odour, the number of spiders that entered the Y maze after seeing mosquitoes was not significantly different from the number of spiders that entered the Y maze after seeing lake flies (Fig. 9.4).

However, after seeing mosquitoes, significantly more spiders entered the Y maze when the masked odour was from mosquitoes instead of from lake flies. Likewise, when lake flies were the priming stimulus, significantly more spiders entered the Y maze when the masked odour was from mosquitoes instead of lake flies (Fig. 9.4). On the basis of this evidence, we conclude that *E. culicivora* becomes more inclined to enter the Y maze when the prey odour is from mosquitoes rather than from lake flies.

Discussion

Our results from the conspicuous treatment in Experiment 1 and the unmasked treatment in Experiment 2, along with the findings from earlier research (Jackson et al., 2005), show that *E. culicivora*'s preferred prey are blood-carrying mosquitoes. Regardless of any potential priming stimuli, the number of spiders that found mosquito lures or mosquito odour was significantly higher than the number that found lake-fly lures or lake-fly odour (i.e., when prey was easy to find because it was conspicuous or unmasked, 'finding' can be understood as simply an expression of the spider's prey-choice decisions). However, when prey was harder to find (i.e., in the cryptic and masked treatments), experimental results appear to reveal how mosquitoes are salient to the spider

in the context of selective attention. More spiders found cryptic mosquitoes when primed by the odour of mosquitoes than when primed by the odour of lake flies and more spiders found masked mosquitoes when primed by seeing mosquitoes than when primed by seeing lake flies. Yet there was no evidence that smelling lake flies primed selective attention to the appearance of lake flies or that seeing lake flies primed selective attention to the odour of lake flies. Moreover, these effects were evident regardless of whether spiders had been maintained before experiments on a diet of blood-carrying mosquitoes alone, a diet of lake flies alone or on a mixed diet. These findings suggest that *E. culicivora* is innately predisposed to becoming selectively attentive to blood-carrying mosquitoes after priming.

There is similar evidence, from research with another salticid, *Portia labiata*, of an innate system governing the way in which selective attention is deployed. Salticid species from the genus *Portia* prefer other spiders as prey (Jackson and Pollard, 1996; Jackson and Wilcox, 1998), and *Micromerys* sp. and *Scytodes* sp. are two of the spider species on which *P. labiata* is known to prey in the Philippines (Jackson and Li, 2004). In experiments, *P. labiata* adopted a search image for whichever of these two prey species had recently been encountered. The conventional context in which search-image studies are cast is of a predator acquiring a search image by perceptual learning after repeated encounters with the prey, but a single encounter suffices for making *P. labiata* selectively attentive to *Micromerys* or *Scytodes* (i.e., individuals of *P. labiata* that had no prior experience with these prey became more effective at finding *Micromerys* sp. after feeding on a single individual of *Micromerys* and more effective at finding *Scytodes* sp. after feeding on a single individual of *Scytodes*).

Yet the findings for *E. culicivora* are different because they can be explained only by cross-modal triggering of innate olfactory and visual search images (i.e., instead of *E. culicivora* having full access to the prey during priming, only visual or only olfactory cues were available). In the experiments using *P. labiata*, the predator had full access to the prey and this means that whether the priming cues were same modality, cross modality, or both is uncertain. There is, in fact, a similar uncertainty in much of the literature on search images (for a notable exception, see Bond and Kamil, 2002).

However, specifically cross-modal effects have been shown for *Portia fimbriata*, another spider-eating salticid, as well as for *Habrocestum pulex*, a salticid that prefers ants as prey (i.e., in experiments using *P. fimbriata* and *H. pulex*, as in our experiments using *E. culicivora*, priming effects on selective attention were demonstrated despite there being no prior feeding on the prey). For *Habrocestum pulex* (Clark et al., 2000), chemical cues from specifically ants primed selective attention to visual cues from specifically ants. For *Portia fimbriata* (Jackson et al., 2002), olfactory cues from specifically *Jacksonoides queenslandicus*, another salticid common in the same habitat as *P. fimbriata*, primed selective visual attention to this particular prey species. The findings for *P. fimbriata* and *H. pulex*, like the findings for *E. culicivora*, reveal cross-modal priming effects that are innate, but our work with *E. culicivora* goes a step further by showing that cross-modality priming works in both directions. In Experiment 1, the odour from blood-carrying mosquitoes, but not the odour from lake flies, primed selective attention to vision-based cues from specifically blood-carrying mosquitoes. In Experiment 2, seeing blood-carrying mosquitoes, but not seeing lake flies, primed selective attention to odour-based cues from specifically blood-carrying mosquitoes. Whether cross-modality priming might also work in both directions for *H. pulex* and *P. fimbriata* has not yet been investigated.

In a recent study, VanderSal and Hebets (2007) showed that another salticid, *Habronattus dossenus*, learned to avoid colour associated with heat in the presence of a seismic stimulus, but that there was no apparent learning when the seismic stimulus was absent. Although the results of this study suggest that input from one sensory modality may facilitate learning in another sensory modality, it may be more appropriate to describe the findings for *H. dossenus* as a general-arousal effect rather than an example of selective attention being triggered. This may also be the case in work with *Drosophila* where both olfactory and visual cues assist with learning to avoid a noxious heat stimulus (Guo and Guo, 2005) and where both olfactory and visual cues improve flight control, enabling an insect to fly towards an odour source (Chow and Frye, 2008).

However, showing cross-modality priming of selective attention to a particular type of prey (blood-carrying mosquitoes for *E. culicivora*, *J. queenslandicus* for *P. fimbriata* and ants for *H. pulex*) seems to be revealing something that is cognitive in a

different way. One way of saying this would be that, for these three salticids, olfactory cues call up a visual representation of an expected, but not yet seen, prey and that, for *E. culicivora*, prey appearance calls up an olfactory representation of an expected but not yet smelled prey. Although an objective understanding of what these 'representations' may actually entail remains elusive, well-known studies on the European toad (*Bufo bufo*) suggest that predators may often rely on very specific features of prey appearance (Ewert, 1974). Our results with *E. culicivora* suggest that the saliency of stimuli related to the appearance of blood-carrying mosquitoes increases when the odour of this prey is present and, furthermore, that the saliency of stimuli related to this prey's odour increases after this prey is seen. One of the next steps in our research will be to determine whether, after priming, *E. culicivora* selectively attends to particular salient features of the mosquito, including particular visual features and particular volatile compounds in the odour plume.

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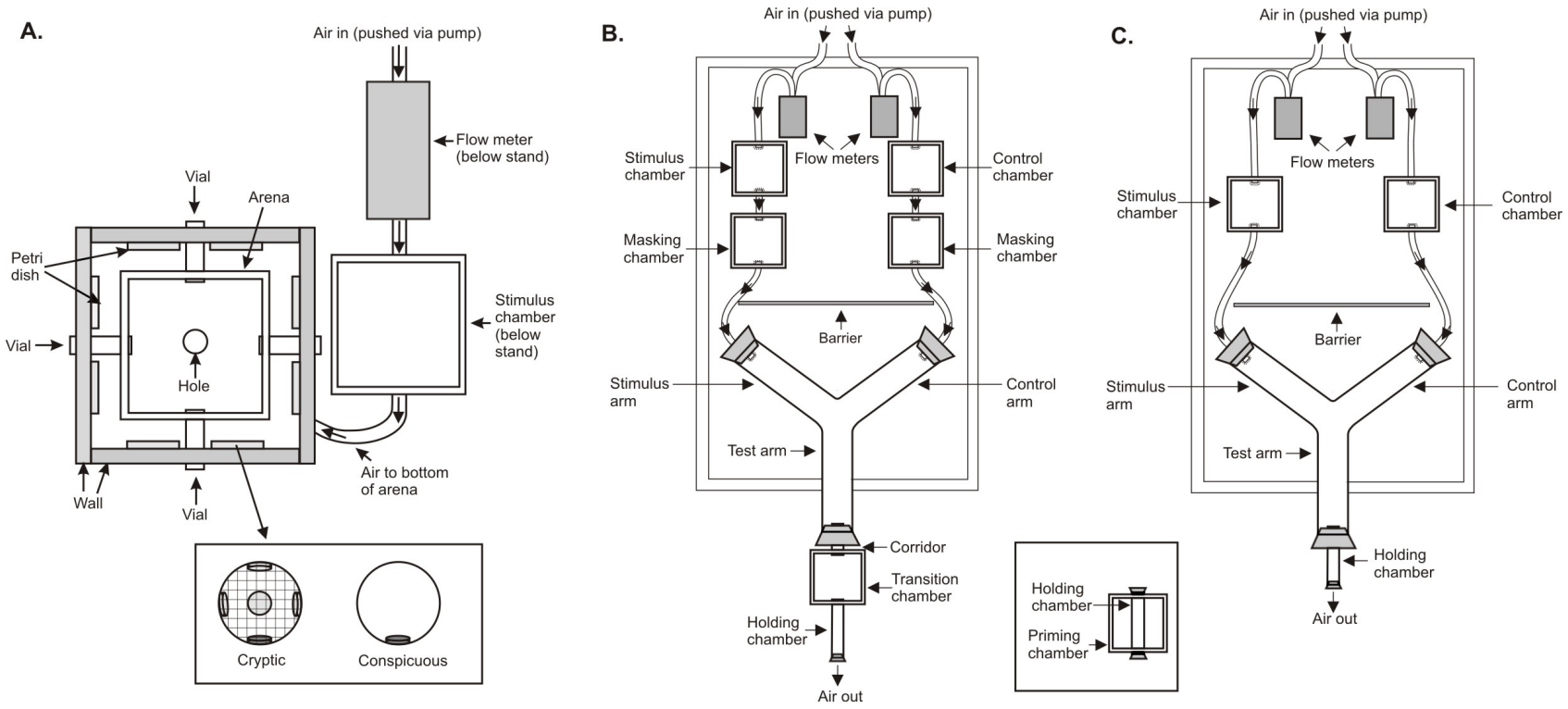
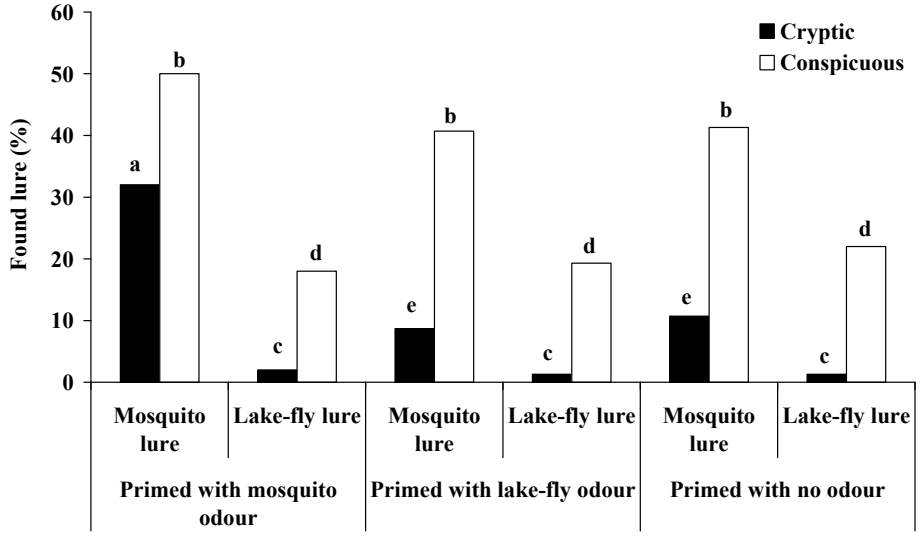


Fig. 9.1. Apparatus for Experiments 1 and 2. Glass chambers used in both experiments (inner dimensions 70 × 70 × 70 mm; thickness 5 mm; removable lid; two holes, diameter 20 mm, on opposite sides) A. Arena for Experiment 1 (not to scale) made of glass (100 mm × 100 mm, walls 35 mm high; removable lid 100 mm × 100 mm). Inset: view of cork discs (diameter 10 mm; thickness 2 mm) from perspective of spider inside box and facing Petri dish. Petri dishes (diameter 35 mm, height 10 mm) held in eight indentations (diameter 36 mm, depth 5 mm) in wall (made of wood; each side 140 mm long, 50 mm high, 10 mm thick) surrounding arena. Lure on

shaded cork disc. Cryptic trials: nylon netting (each square in netting 1.5 mm × 1.5 mm) covers dish; besides disc with lure, another four cork discs present (not shaded). Conspicuous trials: cork disc with lure present; other four cork discs absent; nylon netting absent. Hole (diameter 12 mm): position of hole in lid; a hole in floor of arena directly below (not shown). Odour enters via hole in floor. Test spider (in plastic tube; length 65 mm; internal diameter 11 mm) introduced to arena via hole in lid. Vials (length 50 mm) fitted into holes (diameter 12 mm) centred on four sides of box. Wooden stand (not shown; 300 mm × 300 mm; legs of stand 270 mm long) holding arena hides flow meter, stimulus chamber and odour source situated underneath. B and C. Olfactometer for Experiment 2 with glass Y maze (length of each arm, 90 mm, internal diameter 20 mm). Arrows indicate direction of airflow. Opaque barrier prevents test spider from seeing odour source. Inset: how holding chamber (90 mm long, diameter 20 mm) is positioned inside priming chamber. B. Masked trials. Spider enters test arm by going through transition chamber and corridor (length 40 mm, diameter 20 mm; inner rim flush against inner side of hole in transition chamber) and thereby gaining access to stimulus arm and control arm. C. Unmasked trials. Holding chamber inserted in stopper, providing spider with access to test arm (no masking chambers, no transition chamber).

(A)



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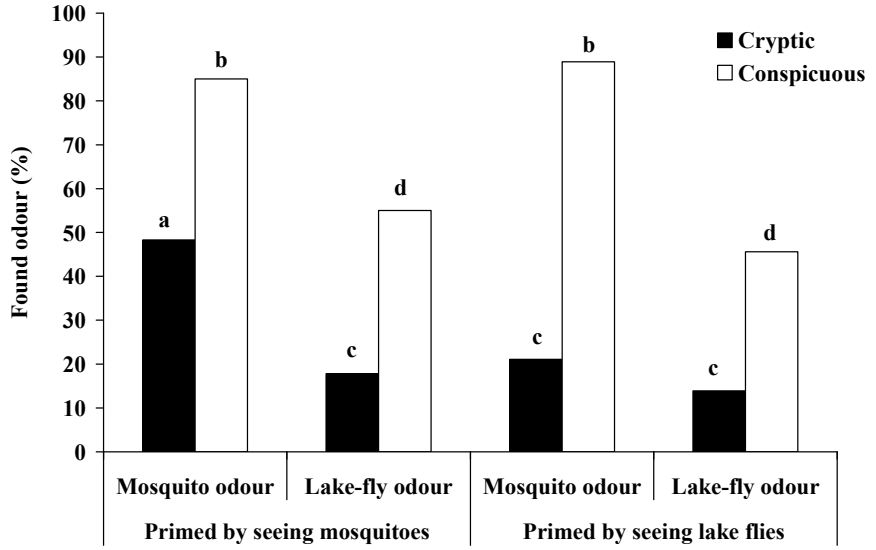
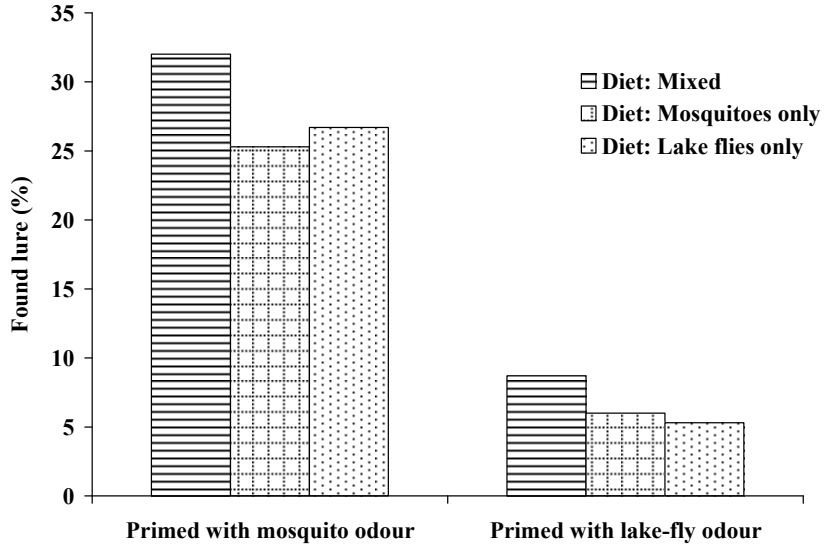


Fig. 9.2. Influence of olfactory priming on how many spiders found lure (cryptic or conspicuous) by sight (A) and influence of visual priming on how many spiders found prey (masked or unmasked) by olfaction (B). All spiders maintained on mixed diet. Letters used to denote statistical significance only for comparisons specified here. Different letters above bars: significantly different (P<0.05). Same letters: not

significantly different (P>0.05). Comparison of finding cryptic or masked vs. conspicuous or unmasked prey: primed with mosquito and found mosquito (A: χ^2 = 10.05, P = 0.002, N = 150; B: χ^2 = 54.45, P<0.001, N = 180), primed with mosquito and found lake fly (A: χ^2 = 21.33, P<0.001, N = 150; B: χ^2 = 53.87, P<0.001, N = 180), primed with lake fly and found mosquito (A: χ^2 = 26.23, P<0.001, N = 150; B: χ^2 = 43.85, P<0.001, N = 180), primed with lake fly and found lake fly (A: χ^2 = 41.33, P<0.001, N = 150; B: χ^2 = 43.21, P<0.001, N = 180), no priming (control) and found mosquito (A: χ^2 = 36.66, P<0.001, N = 150), no priming and found lake fly (A: χ^2 = 31.08, P<0.001, N = 150). Comparison of priming stimulus for finding conspicuous or unmasked prey: found mosquito when primed with mosquito vs. lake fly (A: χ^2 = 2.64, P = 0.105; B: χ^2 = 1.20, P = 0.274), found lake fly when primed with mosquito vs. lake fly (A: χ^2 = 0.09, P = 0.767; B: χ^2 = 3.21, P = 0.073), found mosquito when primed with mosquito vs. control (A: χ^2 = 2.27, P = 0.132), found lake fly when primed with lake fly vs. control (A: χ^2 = 0.33, P = 0.568). Comparison of priming stimulus for finding cryptic or masked prey: found mosquito when primed with mosquito vs. lake fly (A: χ^2 = 25.21, P<0.001; B: χ^2 = 29.43, P<0.001), found lake fly when primed with mosquito vs. lake fly (A: χ^2 = 0.20, P = 0.652; B: χ^2 = 1.02, P = 0.312), found mosquito when primed with mosquito vs. control (A: χ^2 = 20.34, P<0.001), found lake fly when primed with lake fly vs. control (A: χ^2 = 0.00, P = 1.000). Comparison of ability to find conspicuous or unmasked mosquito vs. conspicuous or unmasked lake fly: when primed with mosquito (A: χ^2 = 34.22, P = 0.001; B: χ^2 = 38.57, P<0.001), when primed with lake fly (A: χ^2 = 16.25, P = 0.001; B: χ^2 = 76.70, P<0.001), when not primed with odour (A: χ^2 = 12.96, P = 0.001). Comparison of ability to find cryptic or masked mosquito vs. cryptic or masked lake fly: when primed with mosquito (A: χ^2 = 47.84, P<0.001; B: χ^2 = 37.97, P<0.001), when primed with lake fly (A: χ^2 = 8.49, P = 0.004; B: χ^2 = 3.25, P = 0.071), when not primed with odour (A: χ^2 = 11.58, P = 0.001).

(A)



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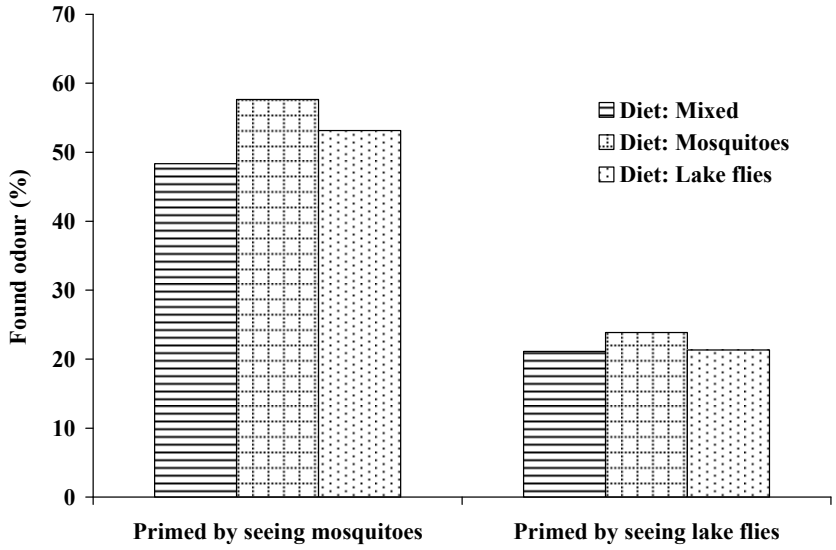

Fig. 9.3. Influence of diet on finding cryptic mosquito lures when primed with mosquito or lake fly odour (Experiment 1) or finding masked mosquito odour when primed by seeing mosquitoes or lake flies (Experiment 2). Comparing mixed diet and mosquito diet: finding mosquito when primed with mosquito (A: $\chi^2 = 1.63$, $P = 0.202$, $N = 150$; B: $\chi^2 = 2.00$, $P = 0.157$, N (mixed diet) = 180; N (mosquito diet) = 85), finding mosquito when

primed with lake fly (A: $\chi^2 = 0.780$, $P = 0.376$, $N = 150$; B: $\chi^2 = 0.26$, $P = 0.610$, N (mixed diet) = 180; N (mosquito diet) = 88). Comparing mixed diet and lake-fly diet: finding mosquito when primed with mosquito (A: $\chi^2 = 1.03$, $P = 0.310$, $N = 150$; B: $\chi^2 = 0.51$, $P = 0.474$, N (mixed diet) = 180; N (lake-fly diet) = 79), finding mosquito when primed with lake fly (A: $\chi^2 = 1.28$, $P = 0.258$, $N = 150$; B: $\chi^2 = 0.00$, $P = 0.964$, N (mixed diet) = 180; N (lake-fly diet) = 89). Comparing mosquito diet and lake-fly diet: finding mosquito when primed with mosquito (A: $\chi^2 = 0.07$, $P = 0.792$, $N = 150$; B: $\chi^2 = 0.33$, $P = 0.564$, N (mosquito diet) = 85; N (lake-fly diet) = 79), finding mosquito when primed with lake fly (A: $\chi^2 = 0.06$, $P = 0.803$, $N = 150$; B: $\chi^2 = 0.16$, $P = 0.689$, N (mosquito diet) = 88; N (lake-fly diet) = 89).

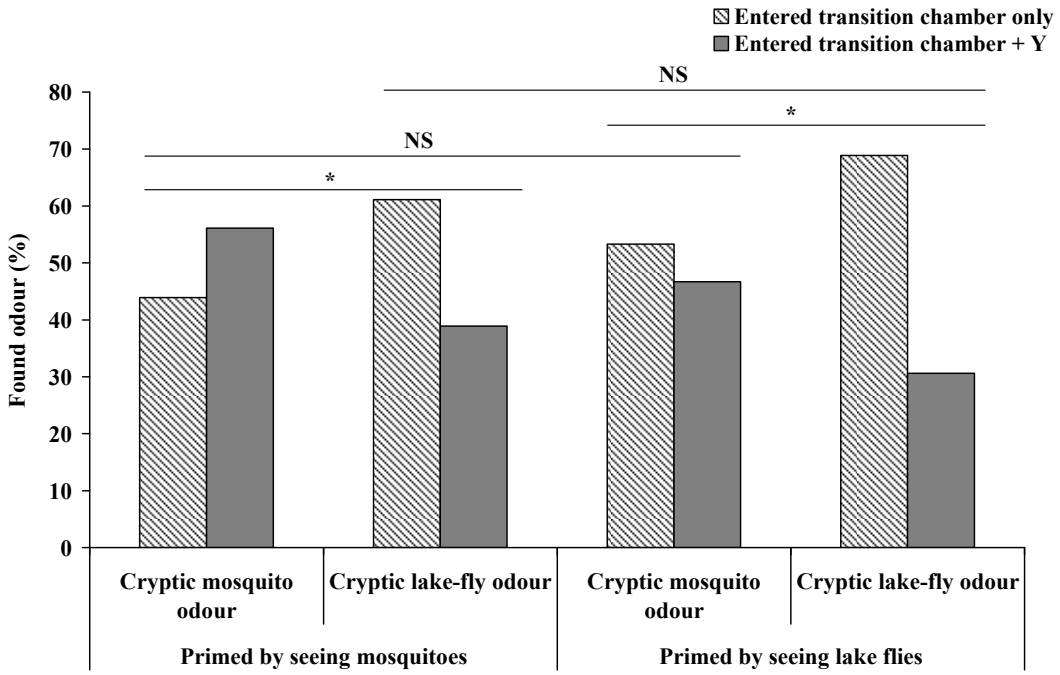

Fig. 9.4. Influence of priming stimulus and of prey odour on *E. culicivora*'s inclination to enter both the transition chamber and Y maze, rather than only the transition chamber (Experiment 2, masked treatment). Primed by seeing mosquitoes vs. lake flies and odour to find was mosquitoes ($\chi^2 = 3.21$, $N = 180$) or lake flies ($\chi^2 = 2.63$, $N = 180$). Odour to find was mosquitoes vs. lake flies and spiders were primed by seeing mosquitoes ($\chi^2 = 10.70$, $N = 180$) or lake flies ($\chi^2 = 9.61$, $N = 180$). NS = Non-significant; * = $P<0.01$.

Chapter 10

Cross-modality effects of prey odour on intraspecific interactions of jumping spiders

In this chapter, I extend the work of Chapters 8 and 9 by considering whether the odour of *Evarcha culicivora*'s preferred prey, blood-carrying mosquitoes, rather than the odour of non-preferred prey, lake flies, primes this salticid for escalating conflict with a rival. In this chapter, I also compare the results for *E. culicivora* with the results for another unusual salticid, *Portia fimbriata*. Spiders from the genus *Portia* specialise at feeding on other spiders, but *P. fimbriata* from Queensland, Australia, appear in particular to single out *Jacksonoides queenslandicus*, another salticid, as preferred prey. In this chapter, I investigate whether, for both *E. culicivora* and *P. fimbriata*, preferred prey are valuable resources worth fighting over.

Evarcha culicivora male hanging from a *Lantana montevidensis* leaf

Cross–modality effects of prey odour on intraspecific interactions of jumping spiders

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Abstract

An important prediction from game theory is that the value of a resource will influence the level to which conflict escalates. An earlier experimental study has shown that males of *Portia fimbriata* and both sexes of *Evarcha culicivora* are primed by the odour of opposite–sex conspecific individuals to escalate conflict with potential rivals (i.e., the spider adopts behaviour that is likely to put it at greater risk of injury after detecting the presence of a potential mate). Another distinctive feature of these two species is that they both have unusual prey-choice behaviour. *P. fimbriata*'s preferred prey is other spiders and *E. culicivora*'s is blood–carrying mosquitoes. Extending earlier work, we investigate whether *P. fimbriata* and *E. culicivora* escalate conflict when in the presence of odour from preferred prey. Our experimental findings show that, for females of *P. fimbriata*, the odour of preferred prey primes escalation of vision–based conflict. However, for males of *P. fimbriata*, and for males and for females of *E. culicivora*, no comparable effect was found.

Key words: aggression; game theory; perception; predation; priming; olfaction; Salticidae

Introduction

Contests between animals are often ranked in terms of their intensity, with higher–ranked contests being associated with greater costs. For instance, making contact during interactions would appear to be especially costly because coming into contact probably puts the animal in harm's way to a greater extent than when displaying from a distance. An important prediction from game theory is that, when animals detect the presence of a valuable resource, they become willing to accept higher contest cost (Dugatkin and Reeve, 1998; Maynard Smith and Parker, 1976; Parker and Rubenstein, 1981) and, in male–male conflict, access to receptive conspecific females often appears to be a resource that drives male escalation decisions. This has been demonstrated experimentally not only for vertebrates (e.g., Verrell, 1986) and crustaceans (e.g., Dowds and Elwood, 1983) but also for spiders (e.g., Austad, 1983; Hack et al., 1997), including jumping spiders (Salticidae) (Cross et al., 2006, 2007b; Elias et al., 2008; Jackson et al., 2006; Wells, 1988).

However, the value of resources often appears to differ for males and for females, as can be seen when the character of male–male aggression differs considerably from the character of female–female aggression (Adamo and Hoy, 1995; Nilsen et al., 2004). For example, male–male contests in *Drosophila melanogaster* appear to be related primarily to competition for access to potential mates, but female–female contests escalate in the presence of yeast, an important food resource for *D. melanogaster* (Dow and von Schilcher, 1975; Spieth, 1974).

Having unique, complex eyes (Blest et al., 1990; Land, 1969a,b) and vision based on exceptional spatial acuity (Harland and Jackson, 2004; Land and Nilsson, 2002), jumping spiders (Salticidae) are especially amenable to experiments on the escalation decisions animals make during contests. It is particularly relevant that,

uniquely among spiders (Rovner, 1989), salticids will threaten and attempt to interact with their own mirror images (Harland et al., 1999). This makes using a mirror a viable alternative to having two same–sex spiders interact in an arena together (see Cross et al., 2007b), thereby avoiding the potentially confounding variables that apply when two living same–sex spiders interact during experiments. However, besides having exceptional eyesight, many salticids are known to make considerable use of chemical cues (Jackson et al., 2002, 2005; Jackson and Pollard, 1997; Pollard et al., 1987), and this suggests that salticids may be especially suitable subjects for research on cross–modality priming (i.e., research on how information from one sensory modality causes attentional changes in another modality; see Calvert et al., 2004; Spence and Driver, 2004). Moreover, a recent study (Cross and Jackson, 2009) highlighted the importance of considering cross–modality priming for salticids in the context of decision making during intraspecific conflict.

Earlier experiments (Cross et al., 2006; Jackson et al., 2006; Wells, 1988) showed that the males of seven salticid species (*Bavia aericeps*, *Euryattus* sp., *Hypoblemum albovittatum*, *Jacksonoides queenslandicus*, *Marpissa marina*, *Portia africana* and *Simaetha paetula*) determine by sight whether a female is a conspecific or a heterospecific and then escalate the intensity with which they interact (i.e., they adopt behaviour that is likely to put them at greater risk of injury after detecting the presence of a conspecific female). Later studies (Cross et al., 2007b; Cross and Jackson, 2009) showed that, for two of these species, *J. queenslandicus* and *P. africana*, and for another two species, *Evarcha culicivora* and *Portia fimbriata*, the odour of conspecific females has cross–modality effects, priming the male to escalate conflict during vision–based male–male interactions. *E. culicivora* is a salticid with unusually pronounced mutual mate choice behaviour (Cross et al., 2007a) and

uniquely, for this species, females are also primed by the odour of conspecific males to escalate conflict when they encounter conspecific same–sex rivals (Cross and Jackson, 2009).

Evarcha culicivora and *Portia fimbriata* are distinctive in another way as well, these being salticids for which it has been demonstrated that prey odour primes selective attention to the vision–based cues from these prey. Both of these species have unusual predatory strategies. *E. culicivora* feeds indirectly on vertebrate blood by actively choosing as preferred prey female mosquitoes that have taken recent blood meals (Jackson et al., 2005, Nelson and Jackson, 2006). Moreover, for *E. culicivora*, the odour of blood–carrying mosquitoes primes selective attention to vision–based cues from blood–carrying mosquitoes, and also vision–based cues from blood–carrying mosquitoes primes selective attention to olfactory cues from blood–carrying mosquitoes (i.e., for this predator, cross–modality priming works both ways; Cross and Jackson, in press).

P. fimbriata is an araneophagic (spider eating) predator (Jackson and Wilcox, 1998) that mobilises a large, flexible repertoire of different prey–specific prey–capture behaviour with which it targets a wide variety of its preferred prey category, other spiders (Harland and Jackson, 2004). In Queensland (Australia), *Jacksonoides queenslandicus* is an especially abundant salticid species (Jackson, 1988) in *P. fimbriata*'s habitat (Jackson and Blest, 1982). The Queensland *Portia* seems to have taken steps toward singling out *J. queenslandicus* as a particularly important prey species. Evidence of this comes from how the odour of *J. queenslandicus* has a priming effect on the Queensland *P. fimbriata*, triggering selective visual attention to the appearance of specifically *J. queenslandicus* (Jackson et al., 2002).

Moreover, when approaching salticid prey, the Queensland *Portia* deploys a unique predatory tactic (Jackson, 1988) called "cryptic stalking", which is based on stealth, careful timing and measures that do not alert the prey to the presence of a predator. *E. culicivora* also moves slowly when preying on blood–carrying mosquitoes, thereby avoiding behaviour that would alert this prey to the presence of potential predators.

For *P. fimbriata* and for *E. culicivora*, *J. queenslandicus* and blood–carrying mosquitoes, respectively, appear to be valuable resources. For these predators, an effective strategy might be to drive rivals away from an area where prey is likely to be encountered, as this should reduce the future risk of interference during attempts at capturing prey. As a step towards testing this prediction, we consider here whether the odour of specific types of prey (*J. queenslandicus* for *P. fimbriata* and blood–carrying mosquitoes for *E. culicivora*) has cross–modal effects on the escalation decisions during intraspecific interactions.

Materials and methods

Basic maintenance and testing procedures

Our experimental subjects were from laboratory cultures (F2 generation) started from specimens collected in western Kenya (*E. culicivora*) and in Queensland (*P. fimbriata*). For details about field sites, see Cross et al. (2008) and Jackson and Hallas (1986). Each individual used as a test spider had been reared in isolation from other salticids using standard rearing and maintenance procedures (for details, see Jackson and Hallas, 1986). All tests were conducted between 0900h and 1500h (lights came on at 0800h and went off at 2000h) using test spiders of standardised size: adult males (body length 8 mm; $N = 30$) and adult females (10 mm; $N = 30$) of *P. fimbriata*; adult

males (body length 5 mm; $N = 30$) and adult females (5 mm; $N = 30$) of *E. culicivora*. As in an earlier study (Jackson et al., 2005), a short pre-trial fast (7 days) was adopted, the rationale for this being to ensure that the test spiders would be motivated to feed during the trials and to standardise the hunger level of test spiders.

Testing methods closely followed those adopted in the earlier studies of olfactory priming (Cross et al., 2007b; Cross and Jackson, 2009). Encounters of a male or a female with its own mirror image ("mirror tests") were staged in a transparent Perspex box (test arena; Fig. 10.1) with a removable glass top. One end of the arena was a mirror. There were two holes (diameter 10 mm) drilled into both side walls, with one hole on each side located near the mirror end and the other hole located at the opposite end of the arena. A silicone tube was inserted in each of these four holes and the ends of the tubes were covered with nylon netting. The holes and tubes were used for airflow from glass chambers situated behind the arena.

As in other recent studies (Cross et al., 2007b; Cross and Jackson, 2009), the airflow system was set up for permeating the entire arena with odour (i.e., we tested for olfactory priming of the salticid's response to its own mirror image). A pump pushed air successively through the silicone tubes into separate stimulus chambers and then, via more silicone tubes, to two holes near the mirror, one on either side of the arena. Airflow was adjusted to 800 ml/min (Matheson FM–1000 flowmeter) and a barrier hid the odour source from the test spider's view. There was no evidence that this airflow setting impaired locomotion or had any adverse effects on the salticid in the arena. Air outflow was through the two matching holes (with silicone tubes attached) at the other end of the arena. A hole (diameter 10 mm) situated in the floor of the arena ("introduction hole"), centred between these two air–exit holes, was used for introducing the test spider.

For experimental tests using *E. culicivora*, both stimulus chambers contained 10 individual blood–carrying *Anopheles gambiae s.s.* females (body length 4.5 mm; fed on blood 4–5 h before used) and, when using *P. fimbriata*, both stimulus chambers contained one adult *J. queenslandicus* female (7 mm; maintained on a diet of house flies and *Drosophila*). For the control tests when using *E. culicivora*, both stimulus chambers contained 10 individuals of another dipteran species, *Nilodorum brevibucca* (Chironomidae) (4.5 mm) and, for control tests when using *P. fimbriata*, both stimulus chambers contained one individual of another salticid species, *Tauala lepidus* (7 mm). Each prey individual was used only once as an odour source. *N. brevibucca* is a prey species of *E. culicivora* in nature and *T. lepidus* is a prey species of *P. fimbriata* in nature, but there was no evidence in earlier olfactometer experiments that *E. culicivora* or *P. fimbriata*, respectively, responded to the odour of these prey (Jackson et al. 2002, 2005). For standardising procedures, all prey used in experimental or control tests were adult females that had reached maturity 5–7 days earlier and had not mated, and all were of standard body length. Test spiders did not have any experience with these prey before experiments.

Stimulus chambers were connected and airflow started 60 min before introducing a salticid ("test spider") into the arena. A test spider was introduced into the arena by first being taken into a transparent glass tube (stopper in each end of the tube) and then keeping the test spider in the stoppered tube for 15–20 min. Next, one of the stoppers was removed and the open end of the tube was fit into the introduction hole. A snug fit was achieved because the tube and hole diameter almost matched. If the test spider had not spontaneously walked out of the tube and into the arena 5 min later, then the other stopper was removed and, using a soft brush, the spider was lightly prodded, whereupon it promptly moved into the arena.

The test spider's entry into the arena defined the beginning of a test and the test spider's first display at the mirror defined the beginning of an interaction. There were rare instances when testing was aborted (never more than 5% of the tests for either species) because the test spider failed to display within 60 min after being introduced into the arena or the test spider entered the arena by running, instead of walking calmly, out of the tube. The end of a test was defined by when the test spider retreated from the mirror and did not return or display again for 30 s. On the rare occasions (< 5% for each species) in which spiders interacted with their mirror image for longer than 30 min, tests were terminated and we recorded the highest rank reached (see below) during the 30–min test period.

Each individual test spider was tested twice (one experimental test and one control test), each time in an arena with a mirror present. For each test spider, the two tests were on successive days. Whether the control or the experimental test came first was decided at random.

Ranking

Based on the level of risk that appeared likely for a salticid performing the display, five ranks for salticid interaction were recognised in earlier studies (Cross et al., 2006, 2007b; Jackson et al., 2006), rank 1 being considered the least costly and rank 5 being considered the most costly. However, when spiders were tested with mirrors, only ranks 1–3 were relevant and only these ranks are considered here (see below for rank descriptions). The rank recorded was the highest reached before one spider (the 'loser') retreated and failed to return. When interacting with mirror images, all test spiders eventually became losers (i.e., mirror images never backed down sooner than the real spider), and the rank reached was interpreted as the level of risk the loser was

willing to accept in a given contest. Below we provide a general characterisation of the three ranks (for species–specific details, see: Cross et al., 2008; Jackson and Hallas, 1986).

Rank 1 (posturing from a distance): distinctive positioning of forelegs (sometimes accompanied by distinctive up–and–down movement of these legs), positioning of chelicerae, positioning of abdomen, walking pattern and entire–body movement.

Rank 2 (propulsive displays): distinctive behaviour by which a spider rapidly closed the distance between itself and the other spider, but with little or no contact.

Rank 3 (face–to–face contact): spiders pushing against each other with the fronts of their cephalothoraxes touching and with each spider's forelegs usually extending out to the side and touching.

Displays that appeared likely to put the displaying spider in little or no danger were ranked lower and displays that appeared to expose the displaying spider to higher risk of injury or death were ranked higher. Although there were instances of spiders, especially *E. culicivora* (see Cross et al., 2008), skipping steps in the ranking, spiders usually behaved as described for each earlier rank before reaching each successive rank.

Data analysis

A score was calculated for each test spider, where the rank attained in the control test was subtracted from the rank attained in the experimental test (i.e., a positive score indicated that the test spider escalated to a higher rank in the experimental test, while a negative number indicated that the test spider escalated to a higher rank in the control test). As each individual test spider was tested twice, the relevant data were the

distribution of scores, not the separate distributions of rank for experimental and control tests. Distribution of scores did not meet the prerequisites for parametric data analysis and, accordingly, we used Wilcoxon matched–pairs tests for data analysis (null hypothesis: score = 0). Using Mann-Whitney *U*-tests, we also compared the scores for different groups of test spiders (null hypothesis: scores for one group of test spiders matched scores for another group of test spiders). Bonferroni adjustments were applied whenever there was repeated analysis of the same data. For details about statistical procedures, see Howell (2002).

Results

The escalation level (rank) reached by *P. fimbriata* females in the presence of *J. queenslandicus* odour was significantly higher than the rank reached in the presence of *T. lepidus* odour ($Z = 2.51$, $P = 0.012$). However, the rank reached by *P. fimbriata* males in the presence of *J. queenslandicus* odour was not significantly different from the rank reached in the presence of *T. lepidus* odour ($Z = 0.27$, $P = 0.790$) (Fig. 10.2). For *E. culicivora* (females and males), ranks in the presence of blood–carrying *A. gambiae* female odour were not significantly different from ranks in the presence of *N. brevibucca* odour (*E. culicivora* females: $Z = 1.05$, $P = 0.294$; *E. culicivora* males: $Z = 0.40$, $P = 0.689$; Fig. 10.3).

Scores for *P. fimbriata* females were significantly higher than scores for *P. fimbriata* males ($Z = 2.29$, $P = 0.044$), but scores for *P. fimbriata* females were not significantly different than scores for *E. culicivora* females ($Z = 1.82$, $P = 0.138$) or scores for *E. culicivora* males ($Z = 2.22$, $P = 0.053$). Moreover, scores for *E. culicivora* females were not significantly different than scores for *E. culicivora* males ($Z = 0.61$, $P = 0.540$), and scores for *E. culicivora* males were not significantly

different than scores for *P. fimbriata* males ($Z = 0.29$, $P = 0.773$).

Discussion

Detecting the odour of *J. queenslandicus* appears to make *P. fimbriata* females more willing to risk performing dangerous (higher ranked) behaviour patterns, supporting our hypothesis that prey is a resource that matters to *P. fimbriata* females in the context of female–female conflict. On the other hand, our data do not show evidence that *P. fimbriata* males escalate in the presence of *J. queenslandicus* odour or that either sex of *E. culicivora* escalates in the presence of mosquito odour. However, these non-significant findings do not simply show that, for *P. fimbriata* males and for both sexes of *E. culicivora*, prey does not matter as a resource. Perhaps the next step is to modify the experimental design we used for presenting prey odour, or to consider the effect of seeing prey on escalation decisions.

Our results for the Mann-Whitney tests show that scores for *P. fimbriata* females were significantly different from scores for *P. fimbriata* males, suggesting that the effect of prey odour on escalation decisions differs for females and males of this species. It is also of interest that the scores for *P. fimbriata* females were not significantly different from the scores for either sex of *E. culicivora*. This may be a hint that it would be premature to conclude that escalating in the presence of prey odour is characteristic of *P. fimbriata* females but not of *E. culicivora*.

Putting these reservations aside for now, we can examine the implications of concluding that preferred prey is a more valuable resource for *P. fimbriata* females than for *P. fimbriata* males or for both sexes of *E. culicivora*. This conclusion presupposes that access to prey is worth defending, but this assumption should be examined carefully. Perhaps *P. fimbriata* females sometimes compete for a prey

individual of the preferred type (i.e., an individual of *J. queenslandicus*) that is actually close by at the time of the conflict. However, it might be more realistic to envisage escalation of conflict functioning not so much for direct access to the prey itself, but primarily to minimize the risk that, at a later time, another *P. fimbriata* female will become a distraction or otherwise interfere with the delicate process of capturing *J. queenslandicus*, this prey being another animal that, like *P. fimbriata*, has excellent eyesight.

That a missed opportunity to capture prey might matter more for *P. fimbriata* females than for *P. fimbriata* males is, on the whole, consistent with a prevalent trend in spiders for prey to be more important as a resource for females than for males (Givens, 1978; Li and Jackson, 1996). For spiders, prior feeding tends to be strongly linked to female fecundity (Heiling and Herberstein, 1999), whereas male reproductive success tends not to be so strongly linked to prior feeding. It is, however, unusual to find evidence of a conditional strategy based on cross–modality priming being subject to a similar trend.

Yet we still need an explanation for why the importance of eliminating interference by a rival might be greater for *P. fimbriata* females than for either sex of *E. culicivora*. After all, it appears that blood-carrying mosquitoes are of considerable importance to both sexes of *E. culicivora* (Cross and Jackson, in press; Jackson et al., 2005). Comparing mosquitoes with *J. queenslandicus*, we can begin to formulate some hypotheses. Perhaps mosquitoes are less likely to be alarmed by the activity of *E. culicivora* individuals interacting in the vicinity. Moreover, when preoccupied with fighting a rival in the presence of preferred prey, there might be a serious risk of *J. queenslandicus*, a salticid and a predator, turning on *P. fimbriata*, but mosquitoes do not prey on salticids.

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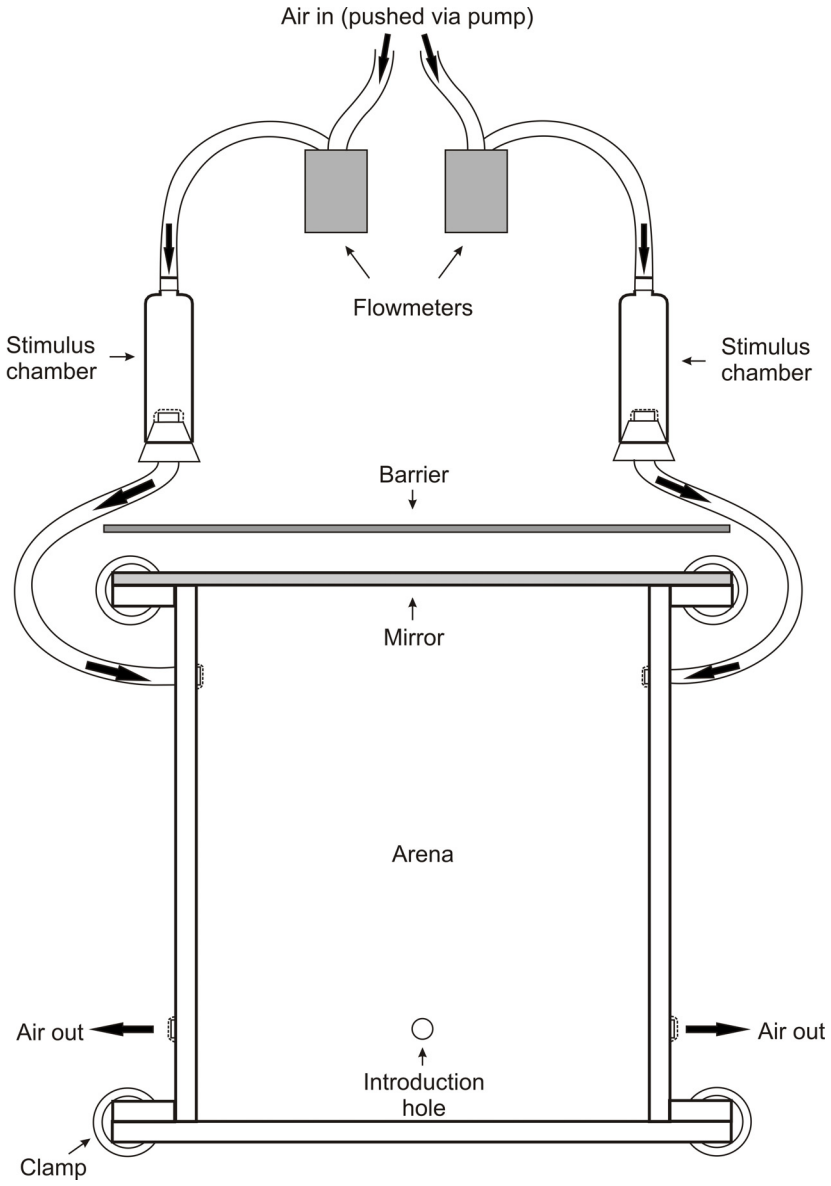

Fig. 10.1. Testing arena (140 mm long × 110 mm wide × 20 mm high; not drawn to scale) made from transparent Perspex. Glass lid not shown. Arrows indicate direction of airflow into arena through silicone tubes. Each of two stimulus chambers (length 115 mm, internal diameter 25 mm) held one prey item (*P. fimbriata*) or 10 prey items (*E. culicivora*). Barrier (opaque plastic) prevented test spiders seeing the prey items used as odour sources. Test spider entered arena through introduction hole. Mirror was one end piece of arena. All end pieces of arena held in place with plastic clamps.

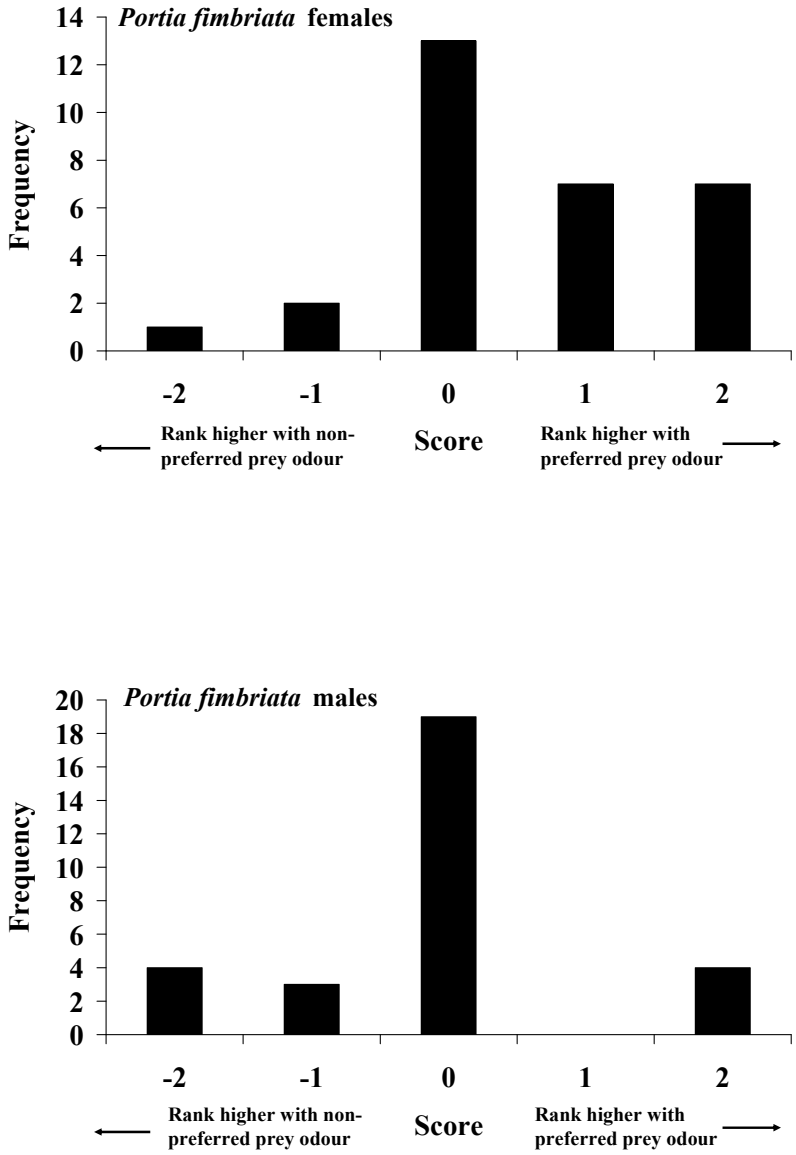

Fig. 10.2. Difference scores attained for females ($N = 30$) and males ($N = 30$) of *Portia fimbriata*. Score: rank attained while exposed to odour of *Jacksonoides queenslandicus* females minus rank attained while exposed to odour of *Tauala lepidus* females.

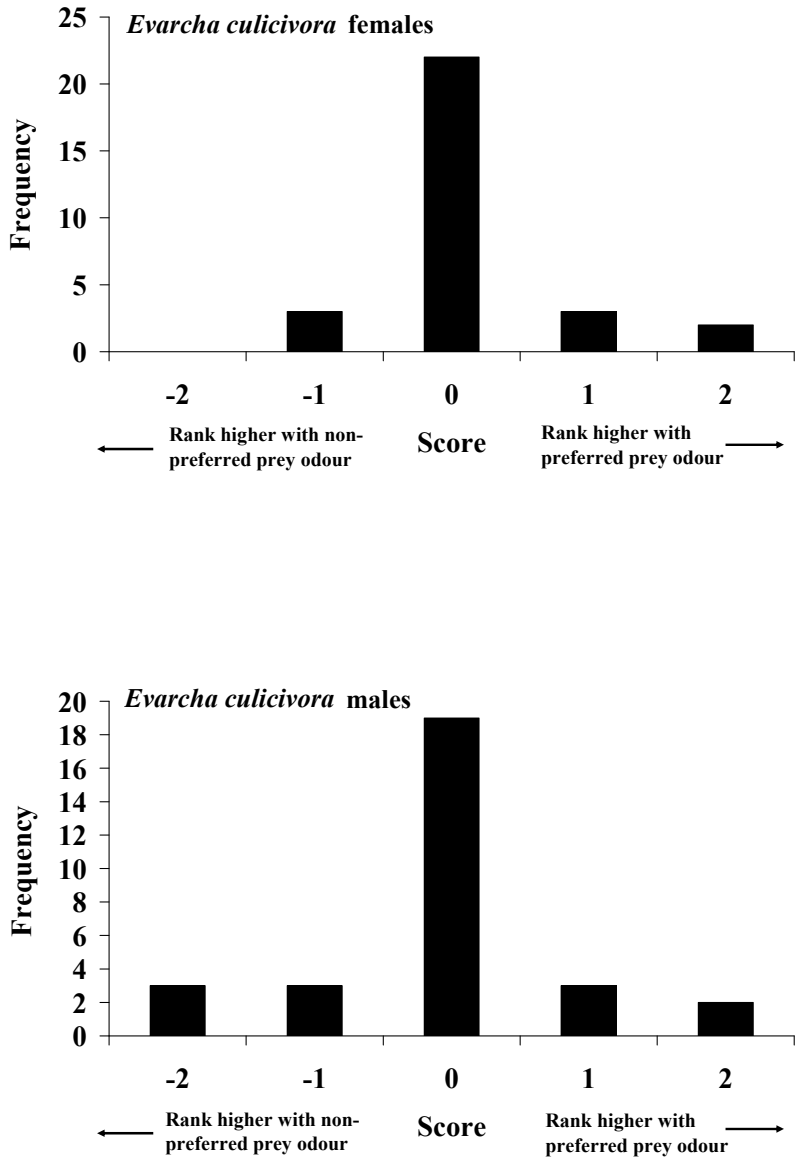

Fig. 10.3. Difference scores attained for females ($N = 30$) and males ($N = 30$) of *Evarcha culicivora*. Score: rank attained while exposed to odour of blood–carrying *Anopheles gambiae s.s*. females minus rank attained while exposed to odour of *Nilodorum brevibucca* females.

Chapter 11

Innate prey-finding and mate-finding search images by *Evarcha culicivora*, a jumping spider from East Africa

Until now, much of the work in my thesis has been about how *Evarcha culicivora* uses olfaction for identifying mates and preferred plants (Chapters 2, 3, 6, 7), for using selective attention to find prey (Chapter 9), and even for making escalation decisions when interacting with a potential rival (Chapters 8 and 10). Although, in Chapter 9, I considered the role of vision in cross-modality priming for finding preferred prey, blood-carrying mosquitoes, until now there has been no evidence that *E. culicivora* uses selective visual attention for finding preferred prey after recently seeing this prey. Also, there has been no evidence that *E. culicivora* uses selective visual attention for finding potential mates after recently encountering potential mates. I consider the role of same-modality priming on *E. culicivora* in Chapter 11. Unlike most search-image studies, where a predator becomes selectively attentive to prey after repeated encounters, in this chapter I consider, as in Chapter 9, whether *E. culicivora* might selectively attend to cryptic prey or mates after only one encounter (i.e., whether search images may be innate rather than learned for this salticid).

Evarcha culicivora male on a *Lantana montevidensis* flower

Innate prey-finding and mate-finding search images by *Evarcha culicivora*, a jumping spider from East Africa

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Short title: Search images by a salticid

Abstract

By choosing blood-carrying mosquitoes as prey, *Evarcha culicivora*, a jumping spider from East Africa, specialises at feeding indirectly on vertebrate blood. This spider also has an unusually complex mate-choice system. Previous studies have shown that *E. culicivora* can identify potential mates and preferred prey by sight alone, whereas here we show that *E. culicivora* uses innate search images for finding potential mates and prey. *E. culicivora* males and females were primed by seeing lures made from blood-carrying mosquitoes or lures made from potential mates, or they were not primed by seeing lures (control), before being introduced into an arena where they had the task of finding either a lure made from a blood-carrying mosquito or a lure made from a potential mate. The lure in the arena was either cryptic (i.e., hidden behind nylon netting and accompanied by distractors) or conspicuous (i.e., netting and distractors absent). When lures were conspicuous, the identity of the priming stimulus appeared to be irrelevant. However, when lures were cryptic, significantly more spiders found mosquitoes after being primed by seeing mosquitoes instead of potential mates and significantly more spiders found potential mates after being primed by seeing potential mates instead of mosquitoes. Moreover, significantly fewer spiders found cryptic mosquitoes after being primed by first seeing potential mates instead of not being primed and significantly fewer spiders found cryptic potential mates after being primed by first seeing mosquitoes instead of not being primed.

Key words: cognition; mate identification; mosquitoes; predation; Salticidae; selective attention

Introduction

If deploying selective attention is cognitively demanding for large animals (Dukas 2004; Dukas and Kamil 2000), including humans (Pashler 1998), it may be argued, intuitively, that these challenges will be especially severe for small animals with small nervous systems (e.g., Bernays 2001). This is part of our rationale for using jumping spiders (Salticidae) as subjects for selective-attention research. However, the sensory system of these spiders' is another important consideration. Jumping spiders have unique, complex eyes and vision based on a level of spatial acuity that is unrivalled by other animals in their size range (Harland and Jackson 2004; Land 1969a, b; Land and Nilsson 2002), and they have often been used in research on vision-based prey and mate identification (Jackson and Pollard 1996, 1997). For example, salticids can be tested with immobile lures instead of living prey (Jackson and Tarsitano 1993), which means we can ascertain whether they have found potential prey in the absence of movement cues and without the actions of the prey individual confounding interpretation of experimental outcome.

Although human based research has been a dominant interest in the literature on attention (e.g., Palmer 1999), biologists have also considered the role of attention with non-human animals, but by another name, 'search images'. This is a term that can be traced back to von Uexküll (1934) (see Bond 2007) but is now most often associated with the hypothesis Lukas Tinbergen used for explaining his field-based data on insectivorous birds (Tinbergen 1960). What Tinbergen envisaged when he wrote about search images was perceptual changes, the idea being that, after a predator has discovered a particular type of prey, it 'gets an eye for' or 'learns to see' this particular type of prey. Although Tinbergen did not phrase his hypothesis specifically in terms of 'attention', it is clear that

'learning to see' refers to a predator being primed to selectively attend to specific features of a particular prey type. This is the context in which the term 'search images' has been used in the more critical research that came after Tinbergen's landmark paper (see Blough 1991; Bond and Kamil 2002; Dawkins 1971a, b; Langley 1996).

Yet much of the literature on search images (see Guilford and Dawkins 1987; Lawrence and Allen 1983) has been unclear about the distinction between selective attention and preference. Showing that a predator prefers a particular prey type is different from showing that a predator has a search image for a particular prey type. Intuitively, a dietary 'preference' refers to what an animal would like to eat (i.e., something that is expressed by choice behaviour), which is not the same as showing that a predator is selectively attentive to features of a particular type of prey (Cross and Jackson 2006; Shettleworth 1998). It is critical to make this distinction by comparing experimental outcomes from trials in which prey is difficult to detect ("cryptic") with experimental outcomes from trials in which prey is easily detected ("conspicuous"). This is because we expect selective attention to matter especially when prey is cryptic. When prey is conspicuous, we expect stronger expression of a predator's preferences because the cognitive demands inherent in deploying selective attention will be less severe.

Here we consider the role of selective attention in the biology of *Evarcha culicivora*, a salticid from the Lake Victoria region of East Africa. This species is unusual because it specialises at feeding on vertebrate blood, gaining access to blood indirectly by choosing blood-carrying mosquitoes as preferred prey (Jackson et al. 2005). However, for *E. culicivora*, this predatory preference may be especially challenging to satisfy. Although mosquitoes are plentiful in this habitat, they are vastly outnumbered by other

mosquito-size dipterans, with non-biting midges, known locally as 'lake flies', from the families Chaoboridae and Chironomidae (Okedi 1992) being especially common. Although *E. culicivora* eats lake flies as well as mosquitoes, the majority of its prey in nature is blood-carrying mosquitoes (Wesolowska and Jackson 2003).

However, search images may be relevant to *E. culicivora* not only in the context of finding its preferred prey. *E. culicivora*'s courtship routine is exceptionally complex, with each sex actively courting the other (Cross et al. 2008) and with both sexes being capable of identifying and choosing mates on the basis of visual cues alone (Cross et al. 2007). Here we consider whether *E. culicivora* uses search images not only in the context of finding prey but also in the context of finding potential mates.

Materials and Methods

General

Our field site and laboratory were in western Kenya (Mbita Point, 0º25´S–0º30´S by 34º10´E–35º15´E, 1200 m above sea level, mean annual temperature of 27º C) at the Thomas Odhiambo Campus of the International Centre of Insect Physiology and Ecology. All spiders were from laboratory culture (F2 generation). Standard spider-laboratory procedures were adopted (see Cross et al. 2008) and all testing was carried out between 0800 h and 1300 h (laboratory photoperiod 12L:12D, lights on at 0700 h). Only critical details are stated here.

With our objective being to investigate innate search images, we ensured that the spiders we used had no prior exposure to mosquitoes or to conspecific individuals by rearing them on a diet of 'lake flies' (fed to satiation 3 times a week on non-biting midges

(Chironomidae and Chaoboridae) collected as needed from the field) and by keeping individuals in separate cages from which no other spiders were visible. As in earlier studies (Jackson et al. 2005; Li and Jackson 1996), a 7-day pre-trial fast was adopted for standardising the hunger level of test spiders.

All spiders used in experiments were adult males and females that had matured 2–3 weeks before used in trials (virgin, body length 4.5 mm). For lures, blood-carrying *Anopheles gambiae ss* (Culicidae) females (body length 4.5 mm) (hereafter referred to as 'mosquitoes') and virgin *E. culicivora* males and females (body length 4.5 mm; hereafter referred to as 'mates') were used. No individual of *E. culicivora* or of *A. gambiae* was used more than once as a test spider or as a lure. Mosquitoes were fed on human blood 4–5 h before being used as lures or for feeding *E. culicivora* (for details, see Jackson et al. 2005).

To make lures, mosquitoes and spiders were first immobilised with CO_2 and then placed in 80% ethanol. The next day, each mosquito or spider was mounted in a life-like posture on the centre of a disc-shaped piece of cork (diameter 10 mm; thickness 2 mm). For preservation, the lure and the cork were then sprayed with a transparent plastic adhesive.

Experimental methods

For distinguishing between effects of selective attention and effects of preference, there were two trial types, 'cryptic' and 'conspicuous' (Fig. 11.1a). In cryptic trials, *E. culicivora* was presented with the task of finding a mosquito lure or mate lure that was behind nylon netting (mesh size, 1.5 mm × 1.5 mm) and accompanied by "distractors"

(i.e., cork discs on which no lure was mounted). Conspicuous trials were like cryptic trials except for the absence of the features (netting and distractors) intended to make the lure difficult to find.

We modified a transparent square arena (Fig. 11.1a) made from glass (100 mm × 100 mm, walls 35 mm high) used in earlier research on mate-choice decisions (Cross et al. 2007). Four glass tubes (length 50 mm, diameter 12 mm) fitted into holes (diameter 12 mm) centred in each of the four sides of the arena. The arena had a removable glass lid (100 mm × 100 mm), with a hole centred in the lid and another hole centred on the bottom ('floor') of the arena (diameter of holes 25 mm). The arena sat on a wooden stand (300 mm × 300 mm; wood thickness 20 mm; legs of stand 270 mm long) and an outer wall (made of wood; each side 140 mm long, 50 mm high, 10 mm thick) was positioned on the stand, surrounding the arena. There was a hole (diameter 12 mm) in the centre of each side of this wooden wall through which the glass tubes protruded (one end of each tube open into the arena; other end closed with a stopper). On either side of each hole in the wall there was an indentation (diameter 36 mm, depth 5 mm), and each indentation held a small Petri dish (height 10 mm) (total: eight Petri dishes around the arena).

In cryptic trials, each Petri dish covered five cork discs. One disc was in the centre (attached with double-sided adhesive tape to centre of indentation in wall). The other four discs were spaced evenly around the rim of the dish, one of these discs being positioned where the dish rim was closest to the floor of the arena ('lower rim position'). The Petri dishes were covered with nylon netting. In conspicuous trials, there was only one cork disc per Petri dish (always in the lower rim position). For both treatments, there was a lure in only one of the Petri dishes and which of the dishes would have a lure was decided

at random for each trial. The disc on which the lure was mounted was always in the lower rim position and the lure was always facing into the arena.

Besides the arena, there were two chambers, a priming chamber and a holding chamber (Fig. 11.1b). The holding chamber was cylindrical (made of 1-mm thick glass; length 70 mm, inner diameter 25 mm), while the priming chamber was cubical (made of 5-mm thick glass, inner dimensions 70 × 70 × 70 mm). The priming chamber had two holes opposite each other, one on the lid and one on the floor of the chamber (diameter of each hole, 25 mm).

Before testing began, the priming chamber was sitting on the lid of the arena, with the hole in the floor of the chamber centred over the hole in the arena lid (Fig. 11.1b). There was no stopper in either of these holes, but there was a rubber stopper in the hole in the lid of the priming chamber, protruding 5 mm into the chamber. The holding chamber, with the test spider inside, was positioned vertically with its lower end fitting snugly in the hole in the lid of the arena and with its upper end covered by the stopper that protruded into the priming chamber. A glass test tube (diameter 25 mm; bottom side up) extended (upside down) through the hole in the floor of the arena so that the closed end of the tube fit firmly against the lower end of the holding chamber, blocking the test spider's access to the arena (hereafter the test tube is referred to as the 'plug'). The plug was held in place with a clamp and stand under the platform on which the arena sat.

In some tests, there were no lures in the priming chamber ('control'), while in other tests there were six lures, one centred on each of the four walls (facing down), as well as one on the floor and one on the ceiling. All six lures were made from either mosquitoes or from potential mates. The lure on the floor and the lure on the ceiling were

positioned so that they faced the centre of floor and ceiling, respectively, and each was positioned so that it was against one of the walls (which of the four walls decided at random) and midway between the two neighbouring walls (Fig. 11.1b).

The test spider was kept in the holding chamber, with lures in view, for 10 min. Then the plug was removed, leaving the lower end of the holding chamber open into the ceiling of the arena, and a rubber stopper was inserted in the hole in the arena floor. Immediately after removing the plug, the priming chamber was lifted away from the arena and holding chamber. A soft brush, pushed through the top end of the holding chamber, was used for gently nudging the test spider so that it walked quietly into the arena. Once the test spider was inside the arena, the holding chamber was removed, the hole in the arena lid was plugged with a rubber stopper and testing began.

Our criterion for recording that the test spider had 'found' the lure was seeing it enter the tube closest to the location of the lure and stay inside for at least 30 s. The rationale for the 30-s proviso was that, in preliminary trials, although *E. culicivora* sometimes entered a tube for a few seconds and then left, any individual that stayed in a tube for 30 s remained in this tube for at least 5 min and any that subsequently left this tube never entered and remained in another tube for as long as 30 s. We also adopted an alternative criterion: *E. culicivora* pressed its face against the side of the arena while facing directly towards the lure, but did not subsequently enter the tube. This criterion was never applicable in more than 10% of the recorded instances of finding a lure in any treatment. Trials ended when *E. culicivora* found the lure or, if *E. culicivora* did not find a lure, until 60 min elapsed.

The entire apparatus was lit with a 200-W incandescent lamp positioned 400 mm overhead and there was additional ambient lighting from overhead fluorescent lamps. Between trials, the apparatus was dismantled and cleaned with 80% ethanol, followed by distilled water, and then dried.

Data analysis

Data were analysed using chi-square tests of independence, Bonferroni adjustments being applied whenever there was repeated testing of the same data sets (see Howell 2002). In all conditions for cryptic and for conspicuous trials, *N* was 200.

Results

Does the cryptic-conspicuous distinction matter?

More spiders found conspicuous than cryptic mosquitoes, with this being significant for trials in which the spider was primed with mosquitoes (males: $\chi^2 = 43.25$, $P<0.001$; females: $\chi^2 = 48.81$, $P<0.001$), primed with mates (males: $\chi^2 = 115.56$, $P<0.001$; females: $\chi^2 = 135.55$, $P<0.001$) or not primed (males: $\chi^2 = 104.45$, $P<0.001$; females: $\chi^2 = 87.56$, $P<0.001$) (Fig. 11.2a, b). Significantly more spiders found conspicuous than cryptic mates in trials in which the spider was primed with mosquitoes (males: $\chi^2 = 168.05$, $P<0.001$; females: $\chi^2 = 116.65$, $P<0.001$), primed with mates (males: $\chi^2 = 79.45$, $P<0.001$; females: $\chi^2 = 58.91$, $P<0.001$) or not primed (males: $\chi^2 = 107.52$, $P<0.001$; females: $\chi^2 = 104.61$, $P<0.001$) (Fig. 11.3a, b). Based on these findings, we are confident that our methods were effective at making lures difficult to find in cryptic trials and easy to find in conspicuous trials.

Does the priming stimulus matter when the lure is conspicuous?

The number of spiders that found conspicuous mosquitoes after being primed with mosquitoes was not significantly different from the number that found conspicuous mosquitoes after being primed with mates (males: $\chi^2 = 0.36$, $P = 0.548$; females: $\chi^2 = 0.21$, $P = 0.645$) or not primed (males: $\chi^2 = 0.65$, $P = 0.420$; females: $\chi^2 = 1.57$, $P = 0.210$). Moreover, the number of spiders that found conspicuous mosquitoes after being primed with mates was not significantly different from the number that found conspicuous mosquitoes after not being primed (males: $\chi^2 = 1.98$, $P = 0.159$; females: $\chi^2 = 0.63$, $P = 0.427$) (Fig. 11.2a, b).

The number of spiders that found conspicuous mates after being primed with mates was not significantly different from the number that found conspicuous mates after being primed with mosquitoes (males: $\chi^2 = 2.40$, $P = 0.121$; females: $\chi^2 = 1.89$, $P = 0.170$) or not primed (males: $\chi^2 = 0.10$, $P = 0.749$; females: $\chi^2 = 2.97$, $P = 0.170$). Moreover, the number of spiders that found conspicuous mates after being primed with mosquitoes was not significantly different from the number that found conspicuous mates after not being primed (males: $\chi^2 = 3.49$, $P = 0.123$; females: $\chi^2 = 0.12$, $P = 0.725$) (Fig. 11.3a, b).

Does the priming stimulus matter when odour is cryptic?

The priming stimulus mattered when lures were cryptic, as significantly more spiders found cryptic mosquitoes after being primed with mosquitoes than after being primed with mates (males: $\chi^2 = 31.92$, $P<0.001$; females: $\chi^2 = 41.26$, $P<0.001$) or after not being primed (males: $\chi^2 = 11.48$, $P = 0.001$; females: $\chi^2 = 17.00$, $P<0.001$). Significantly fewer

spiders found cryptic mosquitoes after being primed with mates than after not being primed (males: $\chi^2 = 6.71$, $P = 0.019$; females: $\chi^2 = 9.70$, $P = 0.004$) (Fig. 11.2a, b).

Significantly more spiders found cryptic mates after being primed with mates than after being primed with mosquitoes (males: $\chi^2 = 42.34$, $P<0.001$; females: $\chi^2 = 30.58$, $P<0.001$) or after not being primed (males: $\chi^2 = 12.70$, $P<0.001$; females: $\chi^2 = 7.44$, $P = 0.013$). Significantly fewer spiders found cryptic mates after being primed with mosquitoes than after not being primed (males: $\chi^2 = 10.64$, $P = 0.002$; females: $\chi^2 = 10.45$, $P = 0.002$) (Fig. 11.3a, b).

Discussion

Findings from the conspicuous treatment in our present study, like the findings from earlier research (Cross et al. 2007; Jackson et al. 2005), support a basic conclusion, that the appearance of blood-carrying mosquitoes and the appearance of potential mates are both particularly salient to *E. culicivora*. However, our goal here was to investigate specifically whether, for *E. culicivora*, prior experience with a particular type of lure (prey or mate) triggers selective attention to that particular type of lure (i.e., we investigated whether *E. culicivora* makes use of search images). Data from our experiments imply that, for *E. culicivora*, finding lures in conspicuous trials is easier than finding lures in cryptic trials. It was only in the cryptic trials where we found evidence that prior experience influenced selective attention for finding mosquitoes or mates and, on this basis, we conclude that *E. culicivora* makes use of prey-finding and mate-finding search images.

This is only the second study to show that a salticid adopts search images, the previous study having been carried out on *Portia labiata* from the Philippines (Jackson and Li 2004). Species from the genus *Portia* are distinctive because they prefer other spiders as prey (Jackson and Pollard 1996; Jackson and Wilcox 1998). *Micromerys* sp. and *Scytodes* sp are two distinctive spider species on which *P. labiata* preys in nature, but the laboratory-reared individuals of *P. labiata* used in the experiments had no prior experience with either of these two prey species. In the experiment, *P. labiata* became more effective at finding cryptic *Micromerys* sp. after feeding once on *Micromerys* sp. and became more effective at finding cryptic *Scytodes* sp. after feeding once on *Scytodes* sp., but there was no evidence that prior exposure influenced how readily *P. labiata* found conspicuous individuals of either prey species (i.e., when prey were conspicuous, *P. labiata* could more readily express its preferences).

The findings in the present study, along with the findings from the search-image study on *P. labiata* (Jackson and Li 2004), depart from the conventional context in which search-image studies are cast. Instead of acquiring a search image by perceptual learning after repeated encounters with a particular type of prey, these two species adopt a search image after a single experience with a priming stimulus. The term "innate search image" appears to be appropriate for what has been shown for these two salticids.

However, the conclusions implied by the research on *E. culicivora* also go a step beyond the conclusions supported by the research on *P. labiata*. We can not be certain that the search images demonstrated for *P. labiata* were primed by strictly visual stimuli, as *P. labiata*'s level of contact included actually capturing and eating the prey. This means we can not rule out the possibility of stimuli in modalities other than vision (e.g.,

olfaction) having a role in priming. Similar uncertainty may often apply to search-image studies where contact from actual feeding has been used as a priming method (for a notable exception, see Bond and Kamil 2002). However, as we precluded any opportunity for *E. culicivora* to feed on mosquitoes or to interact with potential mates in the present study, we are confident that, in our experiments, it was specifically the experience of seeing prey or seeing potential mates that elicited the use of search images.

After priming, *E. culicivora* and *P. labiata* appear not only to become more effective at finding a congruent stimulus, but they also appear to become less effective at finding an incongruent stimulus. This suggests that encountering one type of prey primes *P. labiata* and *E. culicivora* for encountering specifically another individual of the same prey type, not something else (i.e., a different type of prey or a potential mate), and that encountering potential mates primes *E. culicivora* for encountering specifically potential mates, not prey. Even in much bigger animals, such as birds, there may be capacity limits that bring about similar trade-offs and interference effects (Dukas and Kamil 2000; Kamil and Bond 2006), but perhaps not as emphatically as we see with the salticid, a much smaller animal.

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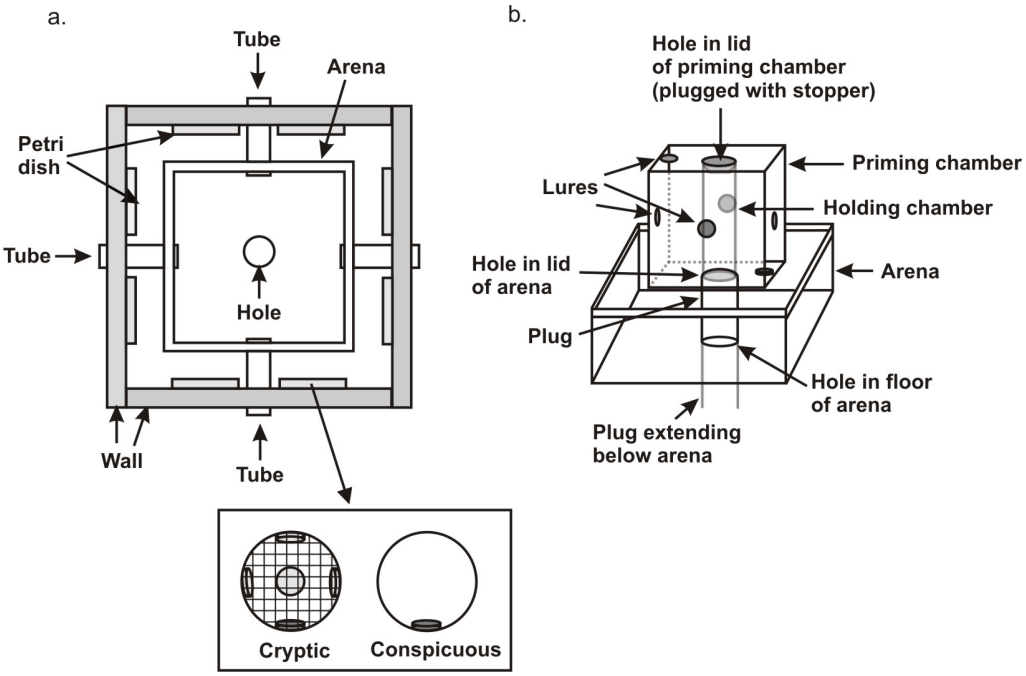
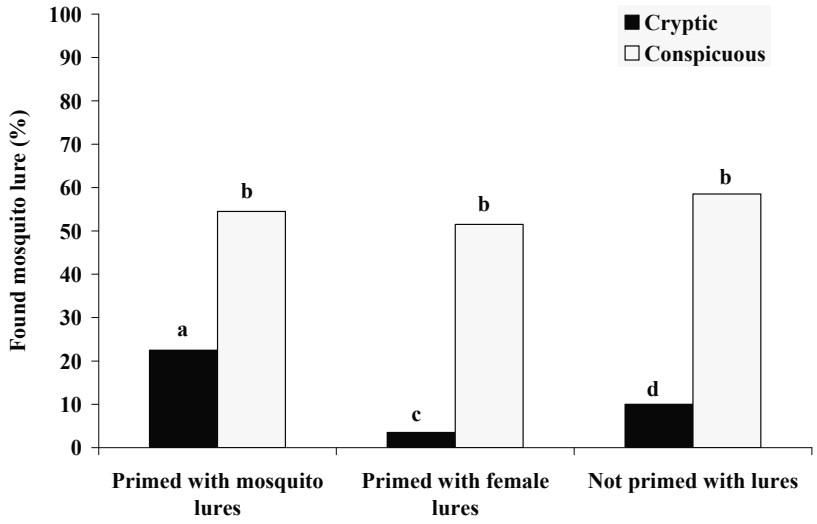


Fig. 11.1. Arena (not to scale) made of glass. Stand (not shown) holds arena. a. Arena viewed from above. Inset: view of cork discs from perspective of spider inside box and facing Petri dish. Lure on shaded cork disc. Cryptic trials: nylon netting covers dish; besides disc with lure, another four cork discs present (not shaded). Conspicuous trials: only disc present is disc with lure (other four cork discs absent; nylon netting absent). Hole: position of hole in lid; a hole in floor of arena directly below. b. Position of holding chamber, priming chamber and plug before spider introduced to arena. Six lures (absent in control tests) inside priming chamber. Clamp holding plug not shown. Tubes attached to arena not shown.

(a)



(b)

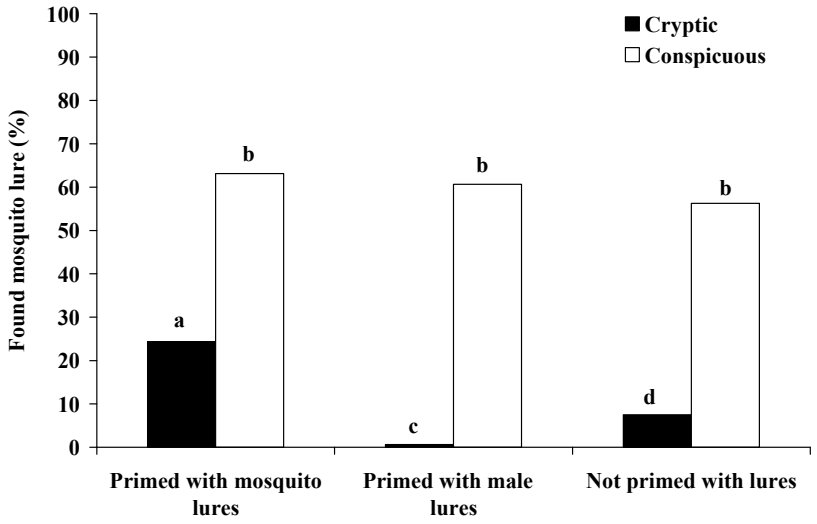
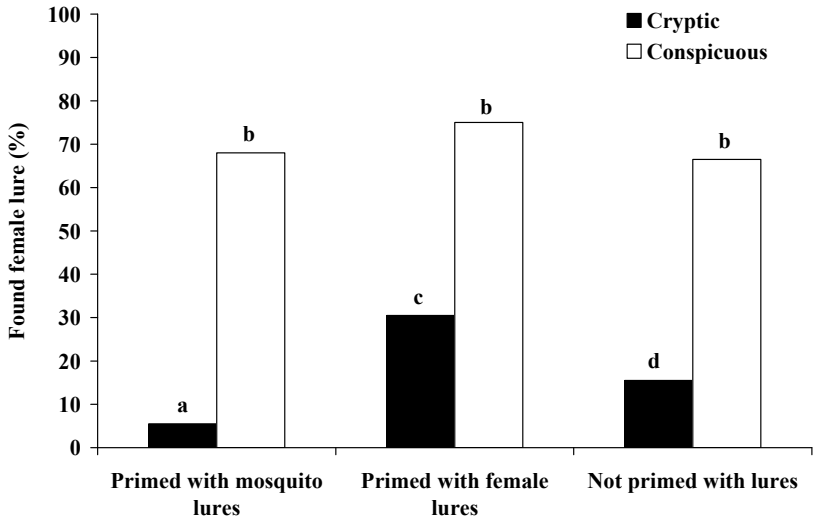


Fig. 11.2. *Evarcha culicivora* males (a) and females (b) that found either cryptic or conspicuous mosquito lures. Before entering arena, spiders primed by seeing lures made from mosquitoes or lures made from potential mates, or were not primed by seeing lures. Different letters above bars denote statistical significance ($P<0.05$); same letters denote non-significance ($P>0.05$).

(a)



(b)

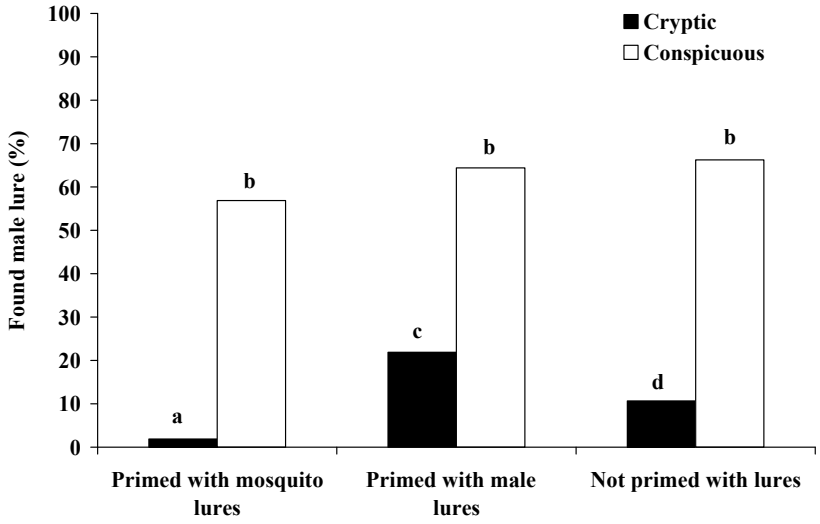
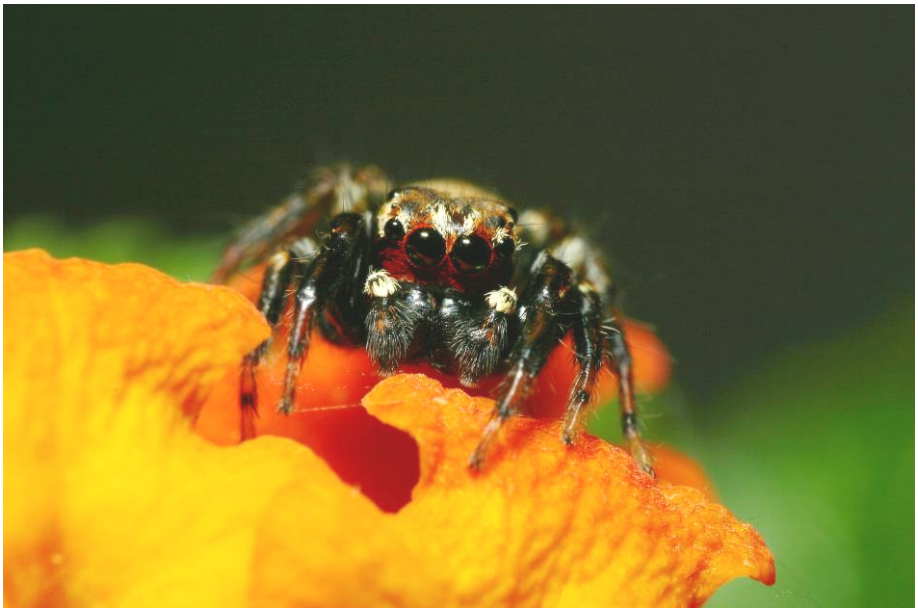


Fig. 11.3. *Evarcha culicivora* males (a) and females (b) that found either cryptic or conspicuous potential mate lures. Before entering arena, spiders primed by seeing lures made from mosquitoes or lures made from potential mates, or were not primed by seeing lures. Different letters above bars denote statistical significance ($P<0.05$); same letters denote non-significance ($P>0.05$).

Chapter 12

Innate olfactory search images for prey and for potential mates by *Evarcha culicivora*, a jumping spider from East Africa

In Chapters 9 and 11, I showed that *Evarcha culicivora* uses search images, both cross-modal (visual and olfactory) and same-modal (visual only), for finding preferred prey. Moreover, in Chapter 11, I showed that *E. culicivora* can even use visual search images for finding potential mates. In Chapters 9 and 11 I also showed that these search images for *E. culicivora* may be innate rather than learned. However, there has been no evidence so far that *E. culicivora* might use olfactory search images for finding prey and mates, and this is what I consider in Chapter 12. There has been very little evidence of olfactory search images with other, much bigger animals, but *E. culicivora* is a salticid that uses olfaction in remarkable, and sometimes surprising, ways (see Chapters 2, 3, 6–9). Furthermore, until now, no studies had considered the role of cryptic odour in olfactory search images. I investigate this, for the first time with any animal, using *E. culicivora*.



Evarcha culicivora male on *Lantana camara* flower

Innate olfactory search images for prey and for potential mates by *Evarcha culicivora*, a jumping spider from East Africa

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Abstract

Evarcha culicivora, a jumping spider from East Africa, specializes at feeding indirectly on vertebrate blood by choosing blood-carrying mosquitoes as prey. It also has an unusually complex mate-choice system. Previous studies have shown that *E. culicivora* can identify potential mates and its preferred prey by odour alone, whereas here we show that *E. culicivora* uses innate olfactory search images. Spiders were presented with the task of finding the odour (either cryptic or conspicuous) of blood-carrying mosquitoes (*Anopheles gambiae*) or the odour of potential mates (i.e. opposite-sex conspecific spiders) after being primed for 10 min with the odour of blood-carrying mosquitoes or the odour of potential mates, or not primed with odour (control). Significantly more spiders found the cryptic odour of mosquitoes when primed by the odour of mosquitoes and significantly more spiders found the cryptic odour of potential mates when primed by the odour of potential mates. Moreover, when primed by the odour of potential mates, significantly fewer spiders found cryptic mosquito odour and, when primed by the odour of mosquitoes, significantly fewer spiders found the cryptic odour of potential mates. Effects of priming were significantly more pronounced in the cryptic than in the conspicuous treatment, as predicted by our hypothesis that the effect of priming is on selective attention instead of preference.

Key words: *Anopheles gambiae*; cognition; *Evarcha culicivora*; jumping spider; mate identification; mosquito; predation; Salticidae; search images; selective attention.

Introduction

Selective attention has long been an important topic in human-based research on cognition (Pashler 1998) but, independent of this tradition in psychology, biologists who study the behaviour of non-human animals have also laboured over the topic of attention, but largely by another name, 'search images'. This term can be traced back to von Uexküll (1934) (see Bond 2007) but it is now most often associated with Tinbergen and the hypothesis he used for explaining his field-based data on insectivorous birds (Tinbergen 1960). Tinbergen (1960) envisaged search images as perceptual changes, the idea being that a predator, after discovering a particular type of prey, 'gets an eye for' or 'learns to see' this particular type of prey. Tinbergen did not phrase his hypothesis explicitly in terms of 'attention', but it is clear that what he meant by 'learning to see' was that previous experience with a particular type of prey primes a predator to become selectively attentive to specific features of this particular type of prey. This is the context in which the term 'search images' has been used in the more critical research subsequent to Tinbergen's landmark paper (see Dawkins 1971a, b; Blough 1991; Langley 1996; Bond & Kamil 2002).

However, Tinbergen's search-image hypothesis has also been the source of considerable confusion (see Lawrence & Allen 1983; Guilford & Dawkins 1987), as researchers have often blurred the distinction between selective attention and preference. Showing that a predator prefers a particular prey type is different from showing that a predator becomes selectively attentive to the features of a particular prey type because, intuitively, a dietary 'preference' refers not simply to what an animal eats but to what it would like to eat (i.e. something that is expressed by choice

behaviour) (Shettleworth 1998; Cross & Jackson 2006). For evidence of the critical distinction between attention and preference, we can compare experimental outcomes from trials in which prey is difficult to detect ('cryptic') with experimental outcomes from trials in which prey is easily detected ('conspicuous'). We expect the influence of selective attention to be especially pronounced when prey is cryptic. When prey is conspicuous, we expect to find the cognitive demands inherent in deploying selective attention to be less severe and that an animal's preferences will be more strongly expressed.

It is not surprising that most of the literature on search images concerns the priming of visual attention, as the term 'images' seems to imply that search images are based, by definition, not on selective attention in general but on visual attention in particular. Yet 'olfactory search images' is a term that sometimes appears in the literature (Nams 1991, 1997; Gazit et al. 2005; see also Melcer & Chiszar 1989), although not so clearly in the context of selective olfactory attention. Our objective is to consider selective olfactory attention and, for this, we need to distinguish between cryptic and conspicuous odour. Perhaps this distinction is particularly elusive when considering olfaction. Nams (1991), for example, did not seem to appreciate the importance of the cryptic-conspicuous distinction and, furthermore, he envisaged 'cryptic' as being a concept that applies more to vision than to the other senses. Yet, by masking a particular odour source, we may achieve the same effect as when crypticity is applied in the context of vision (i.e. we can make an experimental odour source more difficult to detect by pairing it with another odour that is also known to be salient to the test subject).

It has been argued that selective attention is cognitively demanding even for large animals (Dukas 2004), including humans (Pashler 1998), and it seems to follow that, for small animals, with their small nervous systems, the cognitive demands inherent in deploying selective attention will be especially severe (e.g. Bernays 2001). This was part of our rationale for choosing a jumping spider (Salticidae) for search-image research. However, it may not be obvious that a salticid is appropriate for research on olfactory search images in particular. Salticids are better known for having unique, complex eyes and vision based on exceptional spatial acuity (Land & Nilsson 2002; Harland & Jackson 2004). They are frequently used in research on vision-based identification of prey and of conspecific mates and rivals (Jackson & Pollard 1996, 1997), and there is an earlier study showing the use of vision-based search images by a salticid (Jackson & Li 2004). Yet, their extraordinary eyesight notwithstanding, there are numerous examples of salticids using chemical, tactile, auditory and percussion signals, either in conjunction with or as alternatives to vision-based signals (Jackson & Pollard 1997; Elias et al. 2005). Salticids are, in fact, one of the spider families for which we have the most experimental evidence of chemical communication (Pollard et al. 1987; Jackson et al. 2002, 2005).

The salticid species we used in our experiments, *Evarcha culicivora*, is unusual because, by choosing blood-carrying mosquitoes as preferred prey, it specializes at feeding indirectly on vertebrate blood (Jackson et al. 2005). In its natural habitat, the Lake Victoria region of East Africa, satisfying this highly precise predatory preference may be particularly challenging because mosquitoes are vastly outnumbered by 'lake flies', similar-size non-biting midges (Okedi 1992). Yet *E. culicivora* can, with remarkable accuracy, discriminate between lake flies and its

preferred prey, the mosquito. However, the context in which we will consider search images is not only predation but also *E*. c*ulicivora*'s mating system. *E*. *culicivora*'s courtship behaviour is exceptionally complex, with each sex actively courting the other and with both sexes actively making mate-choice decisions (Cross et al. 2007, 2008). Both sexes can also identify opposite-sex conspecific individuals (i.e. potential mates) by olfaction alone (Cross & Jackson in press).

Our hypothesis is that *E*. *culicivora* uses cognitively demanding olfactory search images in the context of finding prey and in the context of finding potential mates.

METHODS

General

Our field site and laboratory were in western Kenya at the Thomas Odhiambo Campus of the International Centre of Insect Physiology and Ecology (Mbita Point). All spiders were from laboratory culture (F2 generation). Standard spider-laboratory procedures were adopted (see Cross et al. 2008) and all testing was carried out between 0800 hours and 1300 hours (laboratory photoperiod 12L:12D, lights on at 0700 hours). Only critical details are stated here.

With our objective being to investigate search images that are innate, we needed spiders that had not experienced exposure to mosquitoes or to conspecific individuals. This was assured by rearing the spiders on a diet of 'lake flies' (fed to

satiation three times a week on non-biting midges (Chironomidae and Chaoboridae) collected as needed from the field) and by keeping each individual in separate cages from which no other spiders were visible. As in earlier studies (Li and Jackson 1996; Jackson et al. 2005), a 7-day pre-trial fast was adopted for standardizing hunger level of test spiders.

All mosquitoes used in experiments were females (virgin, body length 4.5 mm) of *Anopheles gambiae ss* (Culicidae) that were fed on human blood 4–5 h before being used (for details, see Jackson et al. 2005). All test and source spiders were virgin adult males and females (body length 4.5 mm) that had matured 2–3 weeks before used in trials. Source spiders were maintained on a diet of lake flies. No individual of *E. culicivora* or of *A. gambiae* was used more than once as a test spider or as an odour source.

Experimental Methods

We modified a Y-shaped olfactometer used in earlier research on prey-choice decisions (see Jackson et al. 2005). The 'Y maze' was made of glass, with the stem of the Y being the 'test arm', one of the forks of the Y being the 'control arm' and the other fork being the 'stimulus arm' (length of each arm, 90 mm, internal diameter 20 mm). How the apparatus was set up depended on whether the odour was cryptic or conspicuous, but the basic components of the apparatus were the same for the two treatments.

In both treatments, there was a 'stimulus chamber' containing prey (20 mosquitoes) or a potential mate (one conspecific male or female; hereafter referred to as 'mate') connected to the stimulus arm and a 'control' chamber (always empty) connected to the control arm of the Y. There was also a holding chamber in which the test spider was kept before entering the Y and a 'priming-stimulus chamber' that was used for exposing *E. culicivora* to prey or mate odour (Fig. 12.1). The 'holding chambers', and the 'priming chambers' when used for presenting mate odour, were cylindrical (made of 1-mm thick glass; length 90 mm, inner diameter 20 mm), but the rest of chambers used were cubical (made of 5-mm thick glass, inner dimensions 70 × 70 × 70 mm, with a removable lid that provided access to the interior when cleaning). In each cubical chamber, there were two holes opposite each other (diameter 20 mm; centred on side of chamber) and each of these holes was plugged with a rubber stopper. There was a hole in each stopper through which a glass tube (diameter 4 mm) passed and air moved into and out of the chamber through these glass tubes. Silicone tubes connected to the glass tubes bridged airflow between components of the apparatus.

For distinguishing between effects of selective attention and effects of preference, there were two trial types, 'cryptic' and 'conspicuous'. In cryptic trials (Fig. 12.1A), *E. culicivora* was presented with the task of finding prey odour or mate odour in the presence of a masking odour. The masking odour came from a plant (*Lantana camara*) that is highly aromatic and also common in the habitat of *E. culicivora*. The role of the masking odour was to make prey or mate odour more difficult to find ('cryptic'), and the rationale for using *L. camara* as a mask came from other studies showing that *E. culicivora* associates with this plant species (Cross et al.

2008) and is attracted to its odour (Cross & Jackson 2009). Cuttings from *L. camara* (stems, leaves and flowers) were put in two 'masking chambers', one positioned in front of the stimulus chamber and the other in front of the control chamber.

In the cryptic trials, we also used a chamber ('transition chamber') through which *E. culicivora* had to pass before getting close to the odour source (Fig. 12.1A). Inside the transition chamber were four glass pillars (height 70 mm, diameter 25 mm) positioned in the four corners of the chamber, making the space inside the transition chamber more complex. The role of the transition chamber, like the role of the masking odour, was to make finding the prey odour especially difficult for *E. culicivora*. Conspicuous trials were like cryptic trials except for the absence of features intended to make the odour source difficult to find (i.e. there was no masking odour and no transition chamber) (Fig. 12.1B).

A pump coupled to two Matheson FM-1000 flow meters was used for pushing air through the apparatus. Airflow was set at 1500 ml/min and there was no evidence that this airflow setting impaired locomotion or had any other adverse effects on the test spider. In cryptic trials (Fig. 12.1A), air moved independently through the two chambers (i.e. a stimulus chamber and a masking chamber) on one side of the Y and through another two chambers on the other side of the Y (i.e. a control chamber and a masking chamber) and, from the two arms of the Y, air then moved into the test arm. From there, air moved through a glass corridor (length 40 mm, diameter 20 mm) into the transition chamber and then through a holding chamber before exiting through a hole in the stopper. For the conspicuous treatment (Fig. 12.1B), the air path was the

same except that there was no corridor, no transition chamber and no masking chambers.

For each trial, whether the stimulus chamber was on the left or the right side was decided at random. The silicone tubes connecting the chambers to the Y maze were covered with nylon netting on the end facing into the apparatus, blocking the spider's access to the chambers. An opaque plastic screen was positioned between the arms of the Y and the chambers connected to these arms, ruling out the possibility of the test spider seeing the contents of the stimulus and masking chambers. Prey was put in the stimulus chambers and cuttings from *L. camara* were put in the bottom part of each masking chamber 30 min before trials began. This 30-min period allowed time for air to circulate evenly and ensured that air pressure was comparable throughout the olfactometer. The plant material was collected from the field and, using a microscope, any arthropods visible on the material were removed 60–90 min before the plant material was put in the masking chambers. The material filled half the height of these chambers (i.e. it did not rise above the level of the inflow and outflow holes of the masking chambers).

Before each trial began, the test spider was kept for 10 min inside a holding chamber (Fig. 12.1C), with the holding chamber connected by silicone tubing to a priming-stimulus chamber (either a cubicle chamber with 20 mosquitoes inside or a cylindrical chamber with one conspecific male or female inside; opaque plastic screen between holding and priming chamber hiding odour source from test spider's view; airflow set at 1500 ml/min for pushing air through the priming and holding chambers).

At the end of the 10-min priming interval, the stoppers were removed from the holding chamber. For the conspicuous treatment (Fig. 12.1B), the end of the holding chamber farthest from the location of the test spider was inserted through a hole in a stopper (tight fit) and this stopper was inserted into the open end of the test arm of the Y. The open end of the holding chamber was flush with the end of the stopper inside the Y. For cryptic trials (Fig. 12.1A), the end of the holding chamber farthest from the location of the test spider was inserted into one of the holes in the transition chamber (open end flush with inside of box). For both treatments, a stopper was inserted in the opposite end of the holding chamber.

The test spider was free to walk out of the holding chamber and enter the transition chamber (cryptic trials) or the test arm of the Y (conspicuous trials). Once a test spider entered a transition chamber, it was free to enter the hole on the opposite side. A glass corridor was positioned in this hole (inner rim flush against inner side of the hole). The other end of the corridor fit snugly in a hole in a stopper and this stopper plugged the opening of the test arm of the Y (open end of the tube flush with inner side of stopper). The test spider could move through the corridor and into the test arm.

From the test arm, the test spider could move into the stimulus or the control arm of the Y. If the test spider entered the stimulus arm and remained there for 30 s, the trial ended and the outcome was recorded as the spider having found the experimental odour. Otherwise trials lasted for a maximum of 60 min. There were no

instances of the spider entering the control arm, remaining there for 30 s and then, later, finding the experimental odour.

The entire apparatus was lit with a 200-W incandescent lamp that was positioned 400 mm overhead, with additional ambient lighting coming from overhead fluorescent lamps. Between trials, the apparatus was dismantled and cleaned with 80% ethanol followed by distilled water, and then dried.

Data Analysis

Data were analysed using chi-square tests of independence, Bonferroni adjustments being applied whenever there was repeated testing of the same data sets (see Howell 2002). For each condition of the cryptic and of the conspicuous trials, *N* was always 240.

RESULTS

Does the Cryptic-Conspicuous Distinction Matter?

More spiders found conspicuous mosquito odour than cryptic mosquito odour, with this being significant in trials in which the spider was primed with mosquito odour (males: $\chi^2_1 = 69.34$, $P<0.001$; females: $\chi^2_1 = 86.40$, $P<0.001$), primed with mate odour (males: $\chi^2_1 = 236.89$, $P<0.001$; females: $\chi^2_1 = 208.55$, $P<0.001$) or not primed with odour (males: $\chi^2_1 = 180.23$, $P<0.001$; females: $\chi^2_1 = 176.34$, $P<0.001$) (Fig. 12.2A, B). Likewise, significantly more spiders found conspicuous mate odour than

cryptic mate odour in trials in which the spider was primed with mosquito odour (males: $\chi^2_1 = 251.76$, $P<0.001$; females: $\chi^2_1 = 279.24$, $P<0.001$), primed with mate odour (males: $\chi^2_1 = 91.98$, $P<0.001$; females: $\chi^2_1 = 104.56$, $P<0.001$) or not primed with odour (males: $\chi^2_1 = 183.13$, $P<0.001$; females: $\chi^2_1 = 195.65$, $P<0.001$) (Fig. 12.3A, B). Based on these findings, we are confident that our methods were effective at making odour more difficult to find in the cryptic trials and easier to find in the conspicuous trials.

Does the Priming Stimulus Matter when Odour is Conspicuous?

The number of spiders that found conspicuous mosquito odour after being primed with mosquito odour was not significantly different from the number of spiders that found conspicuous mosquito odour after being primed with mate odour (males: $\chi^2_1 = 3.50$, $P = 0.123$; females: $\chi^2_1 = 2.12$, $P = 0.146$) or after not being primed with odour (males: $\chi^2_1 = 2.37$, $P = 0.124$; females: $\chi^2_1 = 0.28$, $P = 0.596$). Moreover, the number of spiders that found conspicuous mosquito odour after being primed with mate odour was not significantly different from the number that found conspicuous mosquito odour after not being primed with odour (males: $\chi^2_1 = 0.11$, $P = 0.739$; females: $\chi^2_1 = 3.92$, $P = 0.096$) (Fig. 12.2A, B).

The number of males and females that found conspicuous mate odour after being primed with mate odour was not significantly different from the number of spiders that found conspicuous mate odour after being primed with mosquito odour (males: $\chi^2_1 = 0.95$, $P = 0.330$; females: $\chi^2_1 = 0.53$, $P = 0.467$) or after not being primed with odour (males: $\chi^2_1 = 1.40$, $P = 0.237$; females: $\chi^2_1 = 2.91$, $P = 0.176$). Moreover,

the number of males and females that found conspicuous mate odour after being primed with mosquito odour was not significantly different from the number that found conspicuous mate odour after not being primed with odour (males: $\chi^2_1 = 0.04$, $P = 0.834$; females: $\chi^2_1 = 0.96$, $P = 0.327$) (Fig. 12.3A, B).

Does the Priming Stimulus Matter when Odour is Cryptic?

Significantly more spiders found cryptic mosquito odour after being primed with mosquito odour than after being primed with mate odour (males: $\chi^2_1 = 96.11$, $P<0.001$; females: $\chi^2_1 = 53.08$, $P<0.001$) or after not being primed with odour (males: $\chi^2_1 = 51.34$, $P<0.001$; females: $\chi^2_1 = 16.71$, $P<0.001$). Significantly fewer spiders found cryptic mosquito odour after being primed with mate odour than after not being primed with odour (males: $\chi^2_1 = 9.67$, $P = 0.004$; females: $\chi^2_1 = 11.37$, $P = 0.001$) (Fig. 12.2A, B).

Significantly more spiders found cryptic mate odour after being primed with mate odour than after being primed with mosquito odour (males: $\chi^2_1 = 73.82$, $P<0.001$; females: $\chi^2_1 = 61.94$, $P<0.001$) or after not being primed with odour (males: $\chi^2_1 = 33.15$, $P<0.001$; females: $\chi^2_1 = 7.95$, $P = 0.005$). Significantly fewer spiders found cryptic mate odour after being primed with mosquito odour than after not being primed with odour (males: $\chi^2_1 = 11.76$, $P = 0.001$; females: $\chi^2_1 = 31.53$, $P<0.001$) (Fig. 12.3A, B).

Does the Priming Stimulus or Identity of Cryptic Odour Affect E. culicivora*'s Inclination to Enter the Y Maze?*

By comparing the number of spiders that entered the transition chamber and then the Y maze with the number of spiders that entered the transition chamber but then failed to enter the Y, we determined whether *E. culicivora*'s inclination to enter the Y maze was influenced by the odour with which it was primed and whether its inclination to enter the Y was influenced by the odour to be found during testing.

When tested for finding cryptic mosquito odour (Fig. 12.4A, B), significantly more spiders entered the Y maze after being primed with mosquito odour than after being primed with mate odour (males: $\chi^2_1 = 101.40$, $P<0.001$; females: $\chi^2_1 = 75.24$, $P<0.001$) or after not being primed with odour ($\chi^2_1 = 57.94$, $P<0.001$; females: $\chi^2_1 = 32.54$, $P<0.001$) and significantly fewer spiders entered the Y maze after being primed with mate odour than after not being primed with odour (males: $\chi^2_1 = 8.02$, $P = 0.009$; females: $\chi^2_1 = 10.11$, $P = 0.002$).

When tested for finding cryptic mate odour (Fig. 12.4A, B), significantly more spiders entered the Y maze after being primed with mate odour than after being primed with mosquito odour (males: $\chi^2_1 = 69.01$, $P<0.001$; females: $\chi^2_1 = 110.02$, $P<0.001$) or after not being primed with odour (males: $\chi^2_1 = 30.76$, $P<0.001$; females: $\chi^2_1 = 25.31$, $P<0.001$) and significantly fewer spiders entered the Y maze after being primed with mosquito odour than after not being primed with odour (males: $\chi^2_1 = 10.10$, $P = 0.003$; females: $\chi^2_1 = 40.40$, $P<0.001$).

After being primed with mosquito odour (Fig. 12.4A, B), significantly more spiders entered the Y maze when tested for finding cryptic mosquito odour instead of cryptic mate odour (males: $\chi^2_1 = 131.45$, $P<0.001$; females: $\chi^2_1 = 172.33$, $P<0.001$). After being primed with mate odour, significantly more spiders entered the Y maze when tested for finding cryptic mate odour instead of cryptic mosquito odour (males: $\chi^2_1 = 45.51$, $P<0.001$; females: $\chi^2_1 = 31.11$, $P<0.001$).

When not primed with odour, the number of *E. culicivora* males that entered the Y maze when tested for finding cryptic mosquito odour was not significantly different from the number of males that entered the Y-maze when tested for finding cryptic odour of conspecific females ($\chi^2_1 = 2.33$, $P = 0.127$). However, significantly more females entered the Y maze when tested for finding cryptic mosquito odour instead of cryptic odour of conspecific males ($\chi^2_1 = 6.83$, $P = 0.009$).

DISCUSSION

Our findings in the present study corroborate a basic conclusion from earlier research: the odour from blood-carrying mosquitoes and the odour from opposite-sex conspecific individuals are both salient to *E. culicivora* (Jackson et al. 2005; Cross & Jackson in press). However, instead of being designed for determining whether *E. culicivora* can identify prey and mates by odour alone, the experiments in the present study were designed specifically for investigating selective attention. In particular, our objective was to determine whether, for *E. culicivora*, prior experience with a specific odour triggers selective attention to that odour (i.e. we investigated whether *E. culicivora* makes use of olfactory search images).

There has been other research on whether animals adopt olfactory search images. Skunks, once they have learned the odour of a particular type of food, detect this odour in a natural grassy area from greater distances than before learning (Nams 1991, 1997). Another study was based on using dogs that had been trained to locate explosives. After prior exposure to a higher level of TNT, the number of containers holding TNT found by these dogs was significantly greater than after prior exposure to a lower level of TNT (Gazit et al., 2005). In basic respects, our findings are similar to those from the skunk and dog research, as more individuals of *E. culicivora* found the sources of particular odours (i.e. odour from blood-carrying mosquitoes or from mates) after exposure to the same particular odour.

Yet the present study on *E. culicivora* differs from the previous skunk and dog studies because we incorporated a comparison between what happens when odour is cryptic versus what happens when odour is conspicuous. This comparison is critical when we want to determine whether the primary effect of prior experience is on preference or on selective attention (Shettleworth 1998; Cross & Jackson 2006). We can expect especially clear evidence of preference when the stimulus to find is conspicuous (i.e. an animal can readily express its preferences when it can easily find a stimulus, and selective attention will not matter very much) and especially clear evidence of selective attention when the stimulus to find is cryptic (i.e. an animal needs to focus its attention when a stimulus is difficult to find). With *E. culicivora*, the effect of prior experience with particular odours (mosquito odour or mate odour) was evident when the stimulus to find was cryptic but not when it was conspicuous. This implies that the effect of prior experience with a particular odour is primarily on

selective attention, not preference and, on this basis, we conclude that *E. culicivora* is a salticid that makes use of olfactory search images.

That salticids adopt search images, but not specifically olfactory search images, was demonstrated in earlier experiments on *Portia labiata* from the Philippines (Jackson & Li 2004). Salticid species from the genus *Portia* prefer other spiders as prey (Jackson & Pollard 1996; Jackson & Wilcox 1998), with *Micromerys* sp. and *Scytodes* sp. being two especially distinctive prey-spider species of *P. labiata*. Using *P. labiata* from a laboratory culture that had no prior exposure to these prey species, it was shown that, after a single encounter with either species, *P. labiata* became more effective at finding cryptic individuals of the particular species it had previously encountered and less effective at finding cryptic individuals of the other species.

Findings from the earlier research on *P. labiata* and the present research on *E. culicivora* share an unusual implication. The conventional context in which search-image studies are cast is perceptual learning after a number of repeated exposures. However, the term 'innate search image' appears to be appropriate for *P. labiata* and *E. culicivora* because, for priming selective attention to a particular target (a particular type of prey spider for *P. labiata*; prey or mate for *E. culicivora*), a single experience suffices. *P. labiata* appears to be predisposed to deploy selective attention that targets either of two particularly distinctive prey-spider species from its natural diet and *E. culicivora* appears to be predisposed to deploy selective attention that targets either potential mates or blood-carrying mosquitoes.

Another parallel between the findings for *E. culicivora* and the findings for *P. labiata* may be especially revealing. Our results suggest that *E. culicivora*'s ability to find cryptic odour of either type (prey odour or mate odour) is impaired when individuals are primed with an incongruent odour and the findings from the earlier study suggest that *P. labiata*'s ability to find either cryptic prey is impaired when primed by prior experience with incongruent prey. It is as though priming prepares *E. culicivora* or *P. labiata* for one thing and this made it more likely to overlook something else. The trade off suggested by these findings may apply to many animals (Dukas & Kamil 2000; Kamil & Bond 2006), but these trade offs may be especially severe for a salticid, a small animal with a small nervous system.

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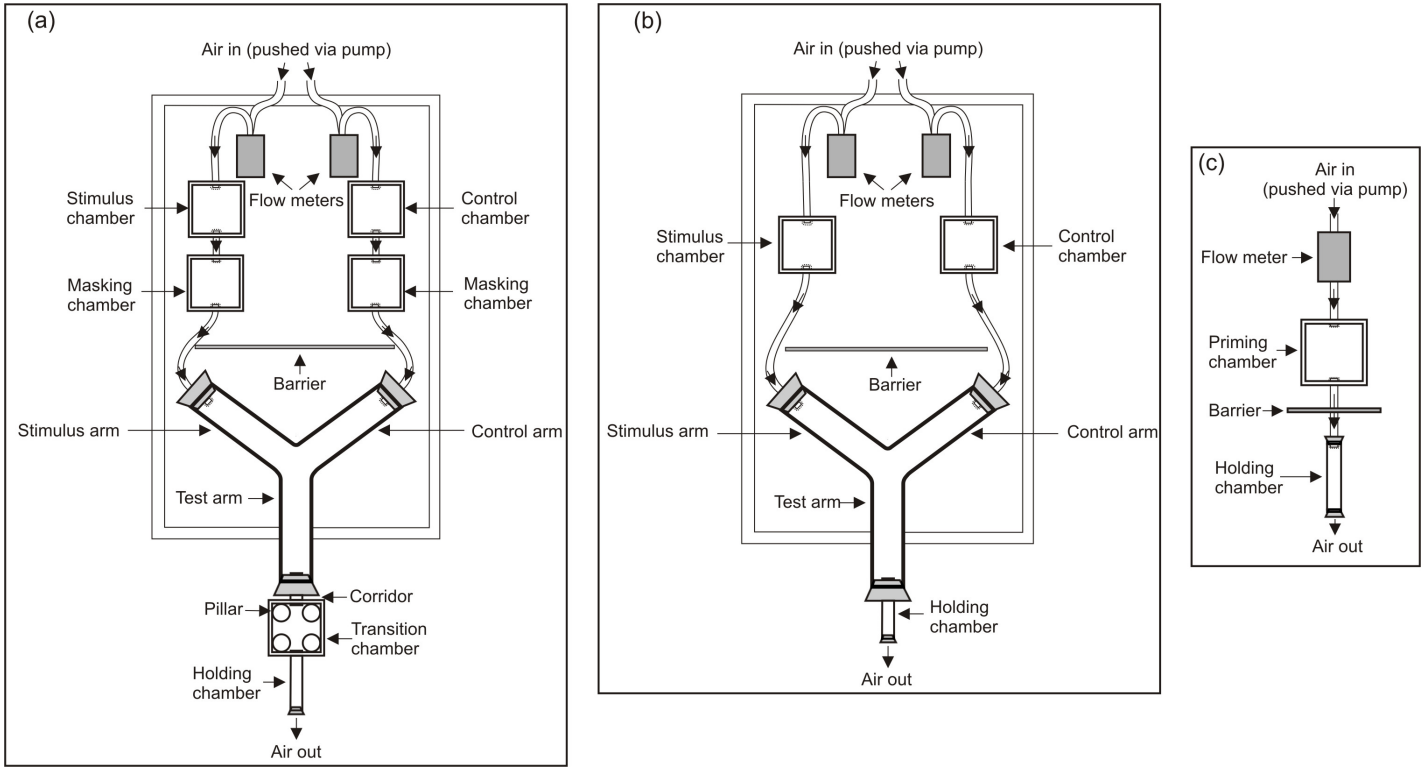
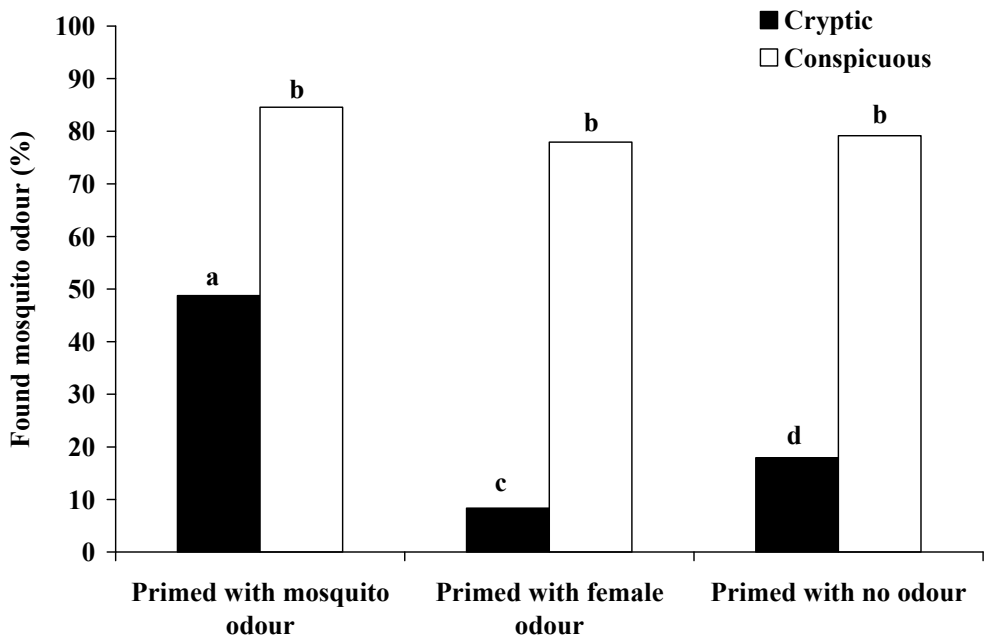


Figure 12.1. Apparatus (not to scale) for cryptic trials (a) and conspicuous trials (b). Arrows indicate direction of airflow. Opaque barriers prevent test spider from seeing odour sources. (c): how holding chamber is attached to priming chamber. (a) Before testing begins, test spider in holding chamber (attached to transition chamber). Start of trial: test spider enters test arm by going through corridor and thereby gaining access to stimulus arm and control arm. (b) Start of trial: test spider in holding chamber; open end of chamber inserted in stopper, providing test spider with access to test arm.

(A)



(B)

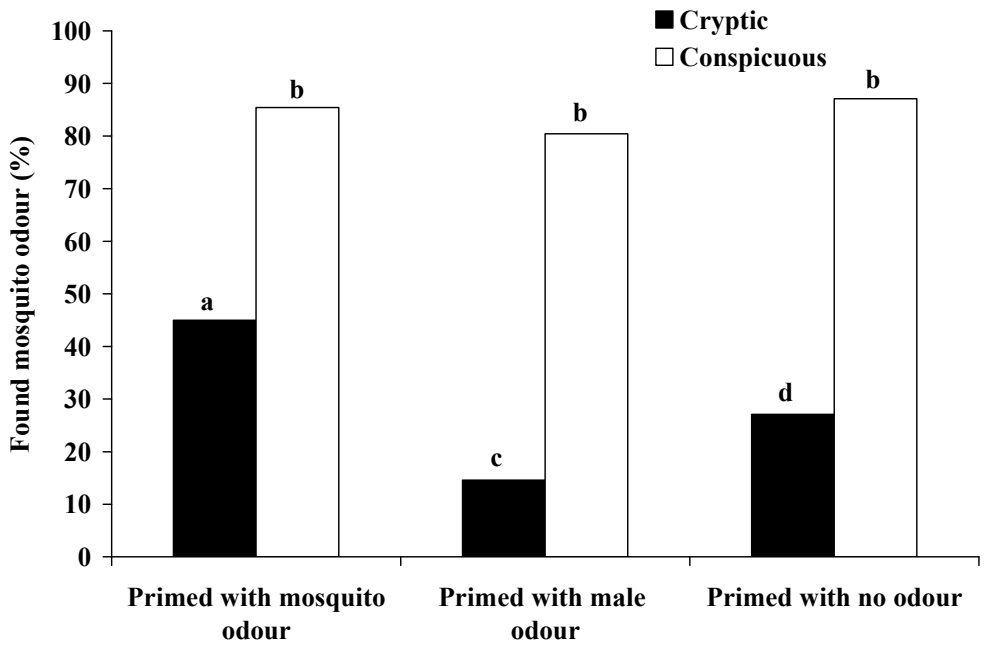
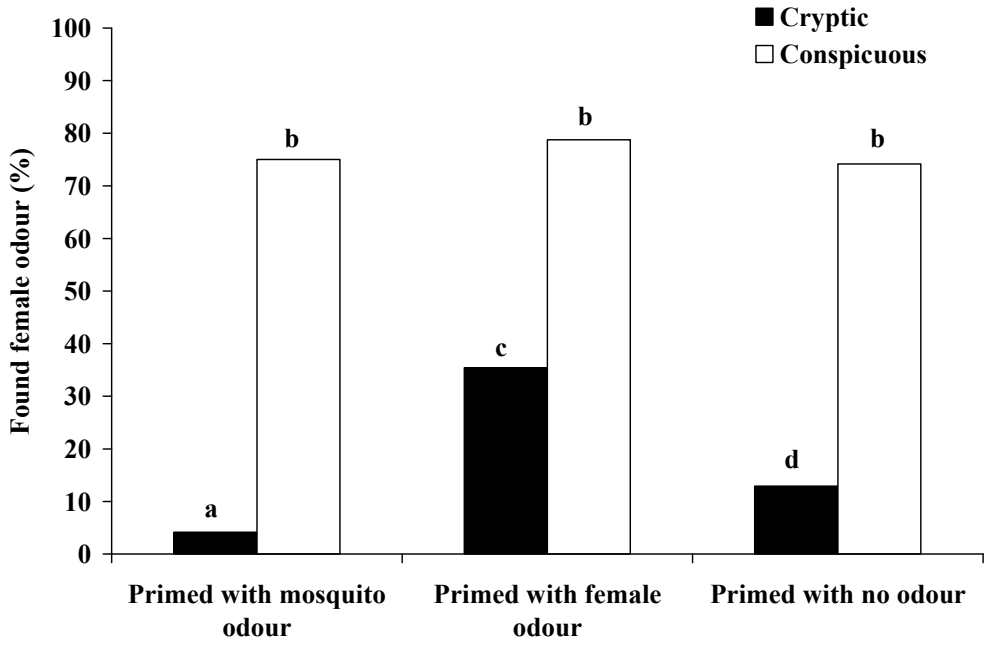


Figure 12.2. Males (A) and females (B) that found either cryptic or conspicuous mosquito odour. Spiders primed with odour of mosquitoes, odour of potential mates or with no odour. Different letters above bars denote statistical significance (P<0.05); same letters denote non-significance (P>0.05).

(A)



(B)

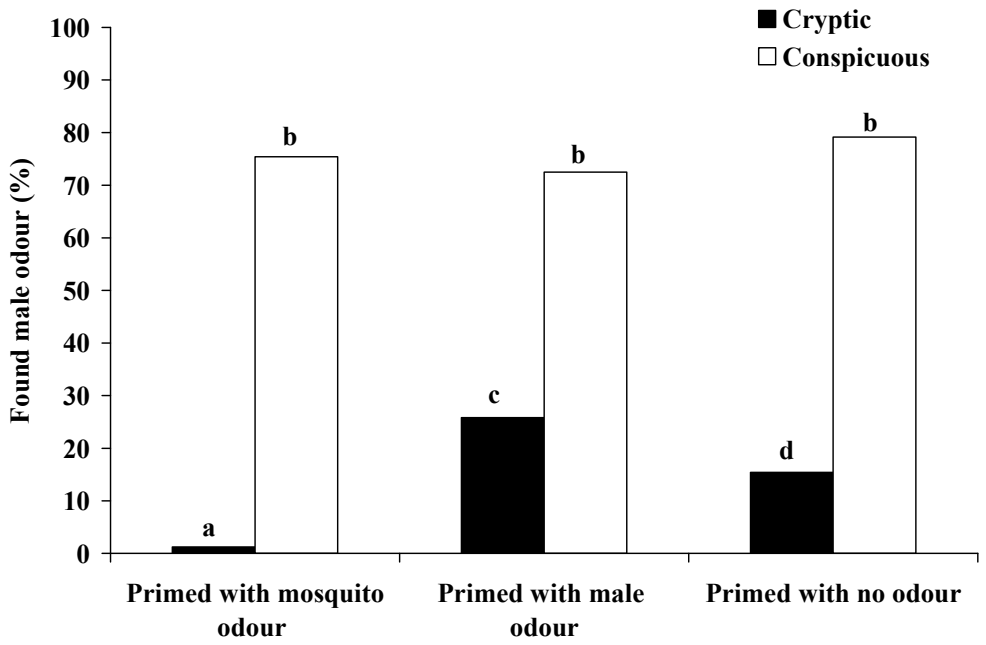
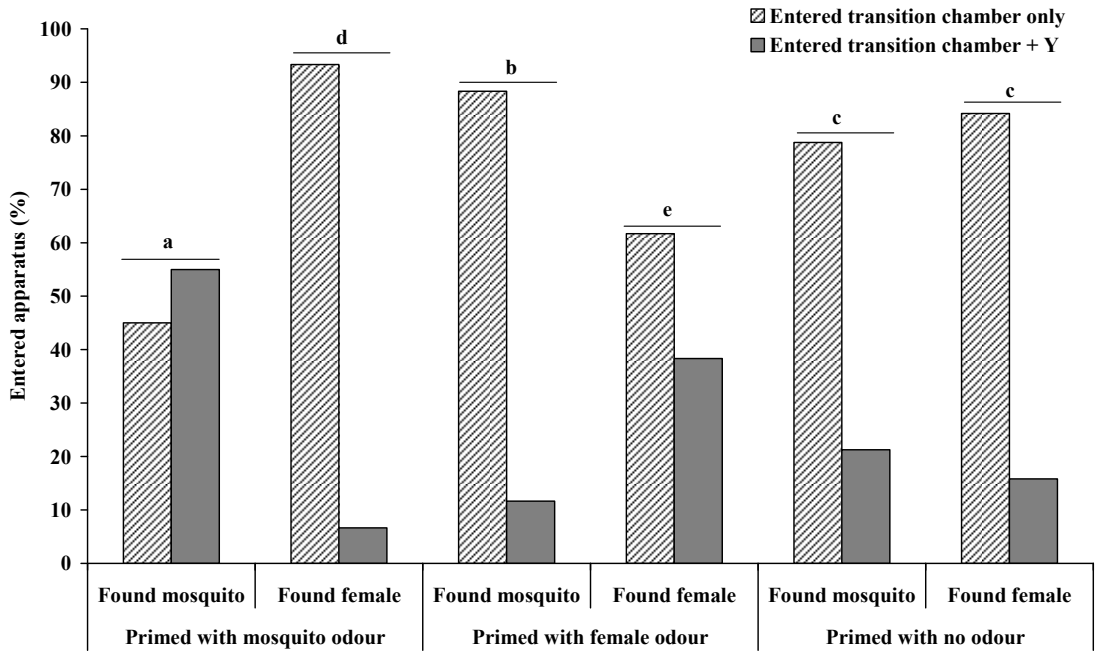


Figure 12.3. Males (A) and females (B) that found either cryptic or conspicuous potential mate odour. Spiders primed with odour of mosquitoes, odour of potential mates or with no odour. Different letters above bars denote statistical significance (P<0.05); same letters denote non-significance (P>0.05).

(A)



(B)

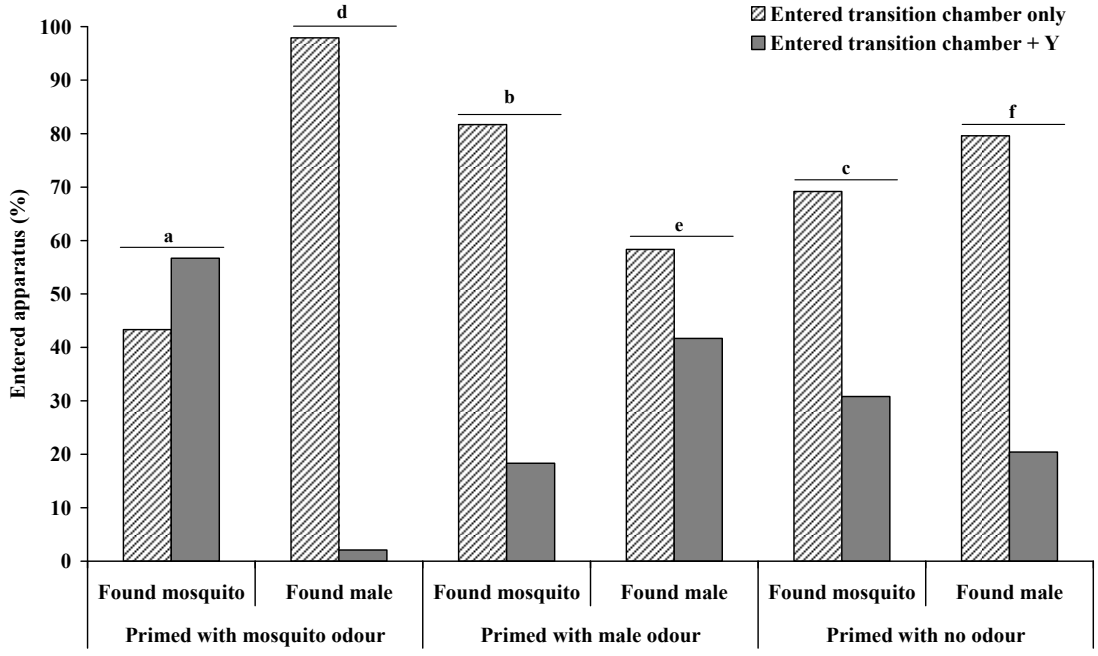


Figure 12.4. Influence of priming stimulus and of cryptic odour on the inclination of *E. culicivora* males (A) and females (B) to enter both the transition chamber and Y maze, rather than only the transition chamber. Different letters above bars denote statistical significance ($P<0.05$); same letters denote non-significance ($P>0.05$).

Chapter 13

Discussion

The other day, I was thinking back to the time when I decided that jumping spiders were boring. The interesting (and embarrassing) thing about it is that, at the time, I didn't even know what a jumping spider was. It's shocking I know, but it's also fair to say that a lot of things have changed since then. Whoever would have thought all those years ago that the very person who said that jumping spiders were boring would end up studying topics relating to selective attention in these very animals? Even I'm surprised by that! These are topics that are more commonly studied in humans and other big-brained animals, not animals with brains that would fit on a pinhead! I have to say, though, that more often than not, it's the spiders that have taught me a thing or two and I've felt like I've just been along for the ride. It's the spiders who are the real stars of the show. And now, because I can no longer leave them alone, they can't leave me alone either.

A day in the life of a Vampire

I'm left with an overwhelming sense that, although it feels like a lot of work has already been done to uncover attentional processes in *Evarcha culicivora*, we have only really scratched the surface. And yet, although the work in Chapters 2–6 was necessary before I could investigate some of these attentional processes in later

chapters, the work in these earlier chapters revealed some insights about *E. culicivora* that were interesting in their own right.

In Chapter 2 I found out, for the first time using a salticid species, that both males and females of *E. culicivora* identify potential mates by odour alone. This supports the previous research that *E. culicivora* makes pronounced use of olfaction (Jackson et al., 2005) and that both sexes of *E. culicivora* are involved in courtship and in choosing mates (Cross et al., 2007, 2008). However, I was intrigued by the result that females apparently lose interest in male odour after they have mated. Something interesting about *E. culicivora* is that males are known to be more cannibalistic than females, with larger males being especially dangerous (Cross et al., 2008). We'd already shown (Cross et al., 2007) that *E. culicivora* females switch preference for smaller, safer, males after mating, and my results for Chapter 2 appears to strengthen this earlier finding that females change their behaviour after mating.

In Chapter 3, however, I apparently unleashed a monster! Here, my results showed that both males and females of *E. culicivora* prefer the odour of potential mates that have recently fed on blood. This shows further evidence of mutual mate choice in this salticid (Cross et al., 2007, 2008), and it also shows an interesting, if gruesome, link between *E. culicivora*'s prey choice and mate choice behaviour. It seems that, by feeding on blood, *E. culicivora* acquires a blood odour or, dare I say, a *perfume*, which it uses to attract the opposite sex. This is a finding that is not only unusual for salticids but also for animals in general. This is also a finding that is likely to keep people awake at night.

The results of Chapter 4 were only preliminary and may even seem mundane in comparison to Chapter 3, but they have sure sparked a whole lot of research ideas with *E. culicivora*! Besides showing that males and females of *E. culicivora* prefer the

draglines from potential mates, one thing I discovered that should be examined further is the possibility that *E. culicivora* determines the size of potential mates, as well as potential rivals, through draglines alone. In Chapter 2, I suggested that mated females might show a greater preference for the odour of smaller males, but here, in Chapter 4, my results suggest that mated females might prefer draglines from smaller males as well. Another particularly interesting finding was that *E. culicivora* males show an aversion to draglines from females of *Portia africana*. *P. africana* is from the same habitat as, and is a potential predator of, *E. culicivora*, but there was no evidence that draglines from *Portia fimbriata*, a closely-related salticid from Malaysia, were aversive to *E. culicivora*. This finding deserves further investigation to determine the extent to which *E. culicivora* avoids draglines from *P. africana* in particular.

Chapters 5 and 6 were a useful start for investigating *E. culicivora*'s possible association with two particular plant species, *Lantana camara* and *Ricinus communis*. In Chapter 5, I found that interactions were especially complex and variable on these plants while in Chapter 6 I found that the odour from each of these two plant species is salient to *E. culicivora*. Although there is a lot more left to be discovered about *E. culicivora*'s association with *L. camara* and *R. communis*, the work in these two chapters establishes an important foundation for how selective attention may be relevant to *E. culicivora* when searching for mates on these plants.

Let's think about these results for a minute. It's quite funny really. Can you imagine how the five year old Fiona would have reacted to hearing that, when she grew up, she would one day be working, basically, with smelly spiders that like smelly plants? Imagine what my teacher would have said! This is stuff that my five year old brain would not have comprehended, even in the wildest realms of my imagination. Yet, unusual though they may be, the first six chapters were important in

showing what stimuli are salient to *E. culicivora*. I already knew that the odour of blood-carrying mosquitoes is particularly salient to *E. culicivora* (Jackson et al., 2005) but here, in the work from these six chapters, I learned that *E. culicivora* is also attracted to the odour from potential mates and from two plant species. Having this knowledge under my belt was very important for developing the work in later chapters.

Eight-legged Einsteins

One thing I was able to test later on was whether the odour of potential mates (Chapter 8) and the odour of blood-carrying mosquitoes (Chapter 10) are of value to *E. culicivora*. In Chapter 8, I found that both males and females show aggression to a potential rival when odour from a potential mate is present. It is unusual to show that salticid females escalate conflict over a potential mate, but my results in this chapter strengthen our evidence that mutual mate choice is pronounced in *E. culicivora* (i.e., in this chapter I found that potential mates are a valuable resource for both sexes of *E. culicivora*).

In Chapter 10, however, I found a possible difference in how two salticid species (*E. culicivora* and *P. fimbriata*) respond to the odour of preferred prey. *P. fimbriata* females showed more aggression to a potential rival when the odour of preferred prey was present, but there was no evidence of this for either males or females of *E. culicivora*. I was surprised by that finding because I assumed that *E. culicivora*'s dietary preference would be difficult to satisfy, making blood-carrying

mosquitoes a particularly valuable resource. Although this result was surprising, it does, however, raise a number of different questions.

The thing about this work is that it gives us some important insights into the value of prey for these two different predators, and one possibility that immediately comes to mind is that perhaps blood-carrying mosquitoes simply aren't as difficult to find in the field as we may be imagining. If *E. culicivora* regularly encounters blood-carrying mosquitoes it might not be so worthwhile to fight with a potential rival over this prey. There is still a lot that we need to uncover on this because we actually don't know how often *E. culicivora* encounters blood-carrying mosquitoes in the field. Perhaps, through this experiment, *E. culicivora* is subtly telling us the answer.

Yet there are other things, different things, about this work that need to be considered. For *E. culicivora*, the hunter becoming the hunted is not a relevant risk, but this risk is very real for *P. fimbriata*, as here the preferred prey are predators (i.e., other salticids) that are fully capable of killing and eating another salticid. If we take this distinction into account and then imagine a situation in which prey may be lurking in the shadows, we might see how driving a potentially-distracting rival away from the vicinity may have benefits that are very different for these two salticids. Compared to *P. fimbriata*, maybe what *E. culicivora* has to gain is considerably less.

But yet another question that needs to be considered is whether *E. culicivora* might escalate conflict over blood-carrying mosquitoes under different circumstances. Perhaps a different experimental design should be considered to determine whether other cues of blood-carrying mosquitoes, such as appearance, may be more salient for inducing escalation of conflict. Although *E. culicivora* is known to make pronounced use of olfaction (Cross & Jackson, in press; see Chapters 2, 3 and 6; Jackson et al., 2005), the issue of a different experimental design probably should be investigated all

the same. Perhaps seeing the bulging red belly of a mosquito really does make all the difference.

It kind of makes me feel like a detective, uncovering all the clues to this mystery. Hopefully, sometime in the future, we'll have a better idea of how we can fit all these clues together. It would be so much easier if somebody had invented for me that little machine for telling me what *E. culicivora* is thinking! Perhaps what *you're* thinking is that I'm asking a lot of questions, and this is all *E. culicivora*'s fault. You never quite know how your experiments will pan out with this animal. *E. culicivora* has this uncanny way of revealing things during experiments that you never expect, but which turn out to be more interesting than you would ever imagine. It makes me think that *E. culicivora* is very special with what it can teach us during the research process (I'd better not also say that *E. culicivora* ought to be awarded a little medal. That would just be weird). You have to give these miniscule animals some credit for how, once you start to understand one thing about this spider, you learn to be ready for an explosion of more research ideas that is always on its way! It leaves you with such an unsettling feeling of there being so much to do and so little time. One thing's for sure, though, it's a weird feeling when you come to the realisation that a jumping spider is your teacher.

Finding a needle in a haystack

Regardless of whether *E. culicivora* escalates conflict over blood-carrying mosquitoes or not, another thing this spider taught me was that it uses selective attention for finding its preferred prey (Chapter 9). In this chapter, I found that smelling or seeing

blood-carrying mosquitoes primes *E. culicivora* for seeing or smelling specifically blood-carrying mosquitoes. It was interesting to find out that, for *E. culicivora*, cross-modality priming works in both directions and I even got the satisfaction of doing something related to my surname. However, the finding in this work that was especially interesting to me was the implication that smelling or seeing blood-carrying mosquitoes apparently calls up in *E. culicivora* an innate search image for finding this particular type of prey.

Most search-image studies are about the priming of visual attention only, and usually very little consideration has been given to whether cross-modality priming might also be relevant. Perhaps a good reason why there are so many studies on visual search images is because of how much we rely on vision ourselves. There does seem to be a bias in the literature, and yet my results in Chapter 11 do suggest that visual search images are relevant for *E. culicivora* (i.e., when *E. culicivora* was primed with seeing one type of lure, it used selective visual attention to find that type of lure again). Being a salticid, *E. culicivora* is highly reliant on vision, and so it does make sense to ask whether this little animal can use selective visual attention.

Yet there's also that nagging possibility that, during the search-image process, cross-modality priming may be more important than many people might actually realise. For example, when an animal is forming a search image for a particular type of prey, it might be obtaining all sorts of information about that prey item, not just visual information. The work in Chapter 9 was important for showing that this might well be the case, and that it's relevant to discuss cross-modality priming in search-image research. The work in this chapter (as well as in Chapters 11 and 12) also showed that an animal does not need repeated exposure to a prey type to form a search image for that prey (i.e., search images can be innate as well as learned). In

other words, *E. culicivora* has challenged some prevalent views of how search images are considered. My little "Einsteins" have done it again!

One thing that's interesting is how I came to do search-image research in the first place. It's weird to reflect on it now, but the thought of doing research on search images actually used to intimidate me a little because of how this topic had become so engulfed with controversy over the years (see Guilford & Dawkins, 1987; Lawrence & Allen, 1983). Trying to redeem it felt like a lost cause. Dawkins (1971) even went so far as to say that we should abandon the term 'search image' altogether because its meaning had become so badly eroded by misuse.

Can you imagine my dilemma? When I started out, I vaguely knew that search images were about animals using selective attention, but here were all these scientists ahead of me practically telling me not to bother with this topic. Imagine what poor Tinbergen had to go through when he first told people his ideas about search images, when people didn't even like to talk about selective attention! It becomes very easy, however, to focus only on the controversy and not on what makes search images so interesting, and I think that's the trap I fell into when I started out. I hadn't fully appreciated what search images are really about. Once I clearly saw the link between search images and selective attention and how this might apply to *E. culicivora*, the rest, shall we say, was history.

I've been interested in topics relating to selective attention for a long time, but my interest began within the realm of human cognitive psychology. I was interested in questions relating to how we pay attention to the world around us. For example, we are surrounded by a multitude of objects on a daily basis, some of which are more relevant to us than others. We have to pay attention to some objects and ignore others. It really staggers me sometimes when I think about the things we take for granted.

How can I, for example, find my set of keys when they are partially concealed by other items on my desk?

There are many theories on visual attention (e.g., see Palmer, 1999), but one theory that I've been interested in for a long time is Treisman's Feature Integration Theory (Treisman, 1986; Treisman & Gelade, 1980). According to Treisman, objects that differ by a simple feature, such as by colour, shape or size, are processed at the same time (i.e., in 'parallel') and we don't need to focus our attention on these features. If, for example, we are presented with an array of coloured circles in a display, all of them being green (the 'distractors') except for one that is red, that red circle (the 'target') is immediately going to "pop out" at us because it immediately strikes us as looking different. It doesn't matter how many circles there are in the display; the target will still pop out, regardless of whether there are only a few distractors or many distractors.

If, on the other hand, the distractors share a conjunction of features with the target, they will look more similar to the target (as would be the case if the target was a red circle and the distractors were green circles and red squares), and focussed attention for finding the target is now essential. Here, we need to serially search through the display until we find the red circle. Hence, the more distractors there are in the display, the longer it's going to take us to find the target (Treisman, 1986; Treisman & Gelade, 1980).

Feature Integration Theory has given us important insights about human visual attention over the years, but there was a nagging sense that gripped me as I learned more and more about these theories in class. I wondered how they might apply to jumping spiders. I should have headed for the hills then and there; it seems that I always take the more arduous path in life! Was I completely and utterly mad? And

yet, the more I thought about it, the more it seemed natural to consider how a spider might pay attention to the world around it. These animals are known for their remarkable eyesight (Harland & Jackson, 2004; Land, 1969a, 1969b) and, for a spider like *E. culicivora*, with its unusual prey preference (Jackson et al., 2005), being attentive to certain prey features would seem advantageous.

Although I'm primarily interested in search images, I can't help but feel if I may have unwittingly started to investigate Feature Integration Theory with a salticid as well. In Experiment 1 of Chapter 9, *E. culicivora* had to search for a prey item, either a blood-carrying mosquito or a lake fly, and then *E. culicivora* had to search for either a blood-carrying mosquito or a potential mate in Chapter 11, all the while surrounded by many distractors in the cryptic trials, but surrounded by only a few distractors in the conspicuous trials. In the conspicuous trials, there were eight cork discs surrounding the arena, with a lure (prey or potential mate) on only one of those discs. Perhaps this prey or mate "popped out" because it looked so different from everything else surrounding *E. culicivora*. This seemed to be the case even when the lure was made from non-preferred prey (i.e., a lake fly; see Chapter 9) and even when the priming stimulus (prey or mate) was incongruent with whether the lure to find was prey or a mate. This might partially explain why so many individuals found the lure in the conspicuous trials.

On the other hand, there were many more cork discs surrounding the arena in the cryptic trials, and there was also netting over the Petri dishes that covered all these discs. The idea here was, by making the lure more difficult to find, focussed attention was much more advantageous, if not essential. The results in Chapters 9 and 11 suggest that being primed with blood-carrying mosquitoes (either by sight or by olfaction) helps *E. culicivora* to focus its attention on finding a lure made from a

blood-carrying mosquito. However, this work should be taken further. The next step is perhaps to vary number of distractors in the cryptic trials and then seeing if our results are similar to typical results for human conjunction search tasks where a person has to look serially through the items in a display. For this, we would want to consider *E. culicivora*'s lure-finding latency, as latency is the primary data when people are the experimental subjects. As I mentioned earlier, humans tend to get slower as the number of distractors increases. Although examining effects of latency has not been informative in these experiments carried out so far with *E. culicivora*, modified methods might be more successful. Besides trying to use data on latency, we still might also discover that fewer spiders find the lures as the distractors increase, and even this finding would be instructive.

With these and other modifications of the experimental methods, we will need to consider carefully whether we have truly given *E. culicivora* a "conjunction search task". When I think about it, I wonder whether the netting that covered the lures is critically important, especially when the lure was a mosquito. We might imagine how the thin strands of the nylon might, for *E. culicivora*, resemble the long, thin features (legs, mouthparts, etc) of a mosquito. More specifically, I wonder if, in the cryptic trials of Chapters 9 and 11, this netting was more distracting to *E. culicivora* than the cork discs. Perhaps the netting was, to *E. culicivora*, actually more "mosquito like" than I had at first appreciated. There's the possibility that what I had in these experiments was even an example of distractors sharing a feature with the target, and this would make the task of finding the lure more like a conjunction search. If this is the case, then maybe I wasn't mad in thinking that Feature Integration Theory might apply to jumping spiders after all.

It certainly would be interesting to investigate the different mosquito features that are, to *E. culicivora*, more "mosquito like" than others. At the end of Chapter 9, I suggested that it would be useful to determine the features (both visual and olfactory) of the mosquito that are salient to *E. culicivora* when searching for this prey. Actually, studies on European toads (*Bufo bufo*) suggest that predators may often pay attention to specific features of prey. For *B. bufo*, a long horizontal line is more salient than a short line, suggesting that length is salient for the toad when searching for worms (Ewert, 1974). This toad work might be a useful source of inspiration for future research on *E. culicivora*.

Images in a spider's mind?

When I mention "mosquito-like" features, it's tempting to wonder if *E. culicivora* compares a mosquito it sees in front of it with a "template" of a prototypical mosquito. Having a template would suggest that *E. culicivora* has a little picture of a mosquito, or a representation of a mosquito, in its mind.

Of course, this is something that could well put people off search-image research. I'm talking about things like spider minds and representations! Do I even want to go there? It might be enough to give a person nightmares. And yet, in human cognitive psychology, there has been a lot of research on mental imagery, such as when people perform mental rotation tasks (Shepard & Metzler, 1971). Also, think about the following question. "Which is further north: Nelson or Wellington?" It just about drives me nuts! I can't get out of my head a picture of New Zealand so that I can compare where Nelson and Wellington are located.

Blough (2006) hopes we can avoid the temptation of thinking that animals conjure up pictures in their heads when they form search images, but others have already considered the possibility (Kamil & Bond, 2006; Langley, 1996). Even the word "image" in "search image" implies imagery, or representation (see Cross & Jackson, 2006). Of course, at this stage there is still a lot that we need to learn about how *E. culicivora* forms search images, and what goes on inside its brain when it pays attention to specific objects in its environment. However, it might not be so silly to think that jumping spiders are capable of having mental representations. Detouring behaviour, where an animal has to take an indirect route to a specific target, has been widely tested in mammals (Chapuis, 1987; Guillaume & Meyerson, 1930; Pongracz et al., 2003; Thorndike, 1911; Wyrwicks, 1959). Yet, in both the field (Jackson & Wilcox, 1998) and in the laboratory (Tarsitano & Andrew, 1999; Tarsitano & Jackson, 1997), a jumping spider, *Portia*, can take convoluted routes to reach a prey item, even routes that require movement away from the prey. By taking detours, this jumping spider needs to plan ahead. What it suggests is that *Portia* acquires a representation of the correct route for reaching the prey, especially important for when that prey is no longer visible (see Cross & Jackson, 2006). For this jumping spider, the results suggest that out of sight doesn't mean out of mind!

One thing that would be interesting to consider is whether the right setting might enhance *E. culicivora*'s ability to find blood-carrying mosquitoes. It was helpful spending some time in Kenya because I could see for myself what *E. culicivora*'s habitat is like, and it made me think about the importance of location for this spider. The thing is that *E. culicivora* tends to hang around people's homes. When they're quiescent, individuals of *E. culicivora* can be found in long grass next to houses, but when they're active they tend to venture indoors. Of course, the sad truth

for the people over there is that malaria is a fact of life, and mosquitoes tend to hang around houses as well, but being inside a house might increase *E. culicivora*'s chances of finding a blood-carrying mosquito. When mosquitoes are heavy with blood, they need to rest and digest their meals. Perhaps mosquitoes rest inside people's houses, and perhaps this is where *E. culicivora* is more likely to find its preferred prey. There is still a lot more about this that needs investigating but, as I suggested earlier, perhaps *E. culicivora* is already teaching us something about how often it encounters this prey. Being at the right place and at the right time would seem critical for *E. culicivora* and, in keeping with the theme of representations, perhaps being inside a house is an important part of the overall picture for finding preferred prey.

During my PhD, I actually did consider the influence of being in the right setting, but this was in the context of *E. culicivora* finding potential mates on plants. When I observed *E. culicivora* on *L. camara* and *R. communis* (Chapter 5), I strongly got the impression that behaviour was more complex and variable than in empty cages, and one thing that struck me in particular was how common it was for individuals to leap about on the plants, especially on *L. camara*. Actually, this was immediately obvious to me when I first sat down to watch a male and a female on a potted *L. camara* – they went crazy! They were like little jumping beans! I recall having so much trouble watching both of them because they leapt about at the same time. Pesky little things! But one thing that struck me more and more was how this leaping often seemed to attract the attention of the other spider. This was how many of the interactions seemed to begin. I didn't notice the spiders leap about so often in empty cages, making me think that this behaviour on the plants might be somehow compensating for being in such a complex environment. It also made me think that

there is something special about *E. culicivora*'s association with *L. camara*, and perhaps even more so than with *R. communis*. For *E. culicivora*, being on *L. camara* might be another part of the overall picture, but this time for finding potential mates.

Although the role of attention isn't usually considered in research on mate choice (see Dukas, 2002), my work with *E. culicivora*, along with research using other salticids (Jackson & Pollard, 1997), suggests that it really should be considered more often. For example, a jungle of leaves and flowers seems like a very difficult environment for orchestrating courtship behaviour, but in this environment it might be easier to attract the attention, and sustain the attention, of an individual by using particularly complex, variable behaviour. Perhaps individuals of *E. culicivora* often meet on plants, and perhaps this is part of the reason why this salticid has the most complex display behaviour ever reported for a spider. When I first had to document all these different behaviour patterns used by *E. culicivora*, I didn't take on board that this spider might be teaching me another thing about selective attention, but this was back in the day when I only observed them in empty cages. The link with selective attention became a lot more obvious when I began watching them on the plants. Even after I had put spiders on plants, I sometimes had difficulty spotting where I'd put them until they began moving around.

Having exaggerated behaviour when on a plant might be important, but it would also be useful to compare how *E. culicivora* behaves when on plants unrelated to *L. camara* or to *R. communis*. Actually, I did consider this using *Heliotropium arborescens* (from the family Boraginaceae), a plant that, to me, looked similar to *L. camara*. My results for this work were too preliminary to include in this thesis, but what I can say is that *E. culicivora* didn't seem as good as finding potential mates on *H. arborescens* as they were on *L. camara*. For one thing, when the spiders were on

H. arborescens their behaviour didn't seem so exaggerated, and they didn't seem to leap about so frequently. It strengthened my impression that this exaggeration in behaviour is an important key for *E. culicivora* when finding potential mates in such a complex environment. Perhaps *E. culicivora* even has an innate strategy for behaving in this way when it's on *L. camara*.

However, there's another thing that perhaps *E. culicivora* is trying to teach us. Perhaps it's the chemistry of the plants that really matters, and perhaps the odour of *L. camara* in particular has a role in priming *E. culicivora* for finding potential mates. Although there's still a lot more we need to learn about *E. culicivora*'s association with *L. camara*, we now know that the odour from this plant is salient to individuals of *E. culicivora* (Chapter 6) and sometimes even triggers courtship display by *E. culicivora* males (Chapter 7). It would be interesting to find out if this odour primes *E. culicivora* for finding potential mates as well. My suspicion from some of this preliminary work is that it probably does. Let the detective work begin!

Kamil and Bond (2006) have discussed how search images are examples of sequential priming (i.e., through repeated exposure to a particular type of prey, a predator becomes selectively attentive to that particular type of prey). They argue that search images are not formed through associative priming (i.e., where a particular cue gives a predator the expectation for finding a particular type of prey). Yet associative priming seems a more relevant explanation for what I've found with *E. culicivora*. For example, the smell of blood-carrying mosquitoes apparently primes individuals for seeing cryptic blood-carrying mosquitoes (Chapter 9) and seeing potential mates primes *E. culicivora* for finding cryptic potential mates again (Chapter 11). Perhaps the odour of *L. camara* primes *E. culicivora* for finding potential mates as well. In all

of these instances, *E. culicivora* evidently needs to use selective attention to find something and, on this basis, it appears that *E. culicivora* uses search images.

However, Kamil and Bond (2006) only discuss literature on much bigger animals, such as birds, and perhaps we simply need a different explanation for how small animals like jumping spiders use search images. At some point, it would be interesting to find out whether *E. culicivora* is any better at finding blood-carrying mosquitoes after sequential priming than after priming with a particular cue. However, I have a feeling that the influence of sequential priming on *E. culicivora* will be more evident when the task is to find non-preferred prey, such as lake flies. For finding non-preferred prey, associative priming does not appear to be enough.

The sweet smell of success

Regardless of what type of priming may be involved with search images, however, my results for Chapter 12 were as I had long suspected: *E. culicivora* are the heroes of olfactory-search-image research! These little animals showed that when they were primed with a particular odour, they used selective attention to find that odour in an olfactometer even when it was masked by the odour of *L. camara*. To the best of my knowledge, this is the first experiment that has considered whether olfactory search images are relevant when odour is cryptic versus conspicuous.

It's interesting, because my preliminary results in Chapter 7 indicated that the odour of potential mates and the odour of blood-carrying mosquitoes both trigger courtship display and even more disturbing was the finding in Chapter 3 that feeding on blood makes individuals of *E. culicivora* more attractive to the opposite sex. The

results from these chapters suggest that the odour of potential mates and the odour of blood-carrying mosquitoes are both relevant to *E. culicivora* in the context of mate choice. Yet in the cryptic trials of Chapter 12 I didn't find that the odour of blood-carrying mosquitoes primed *E. culicivora* to find the odour of potential mates. It would have been bizarre to get that finding, and it would have made *E. culicivora* all the more terrifying, but you can be rest assured that this doesn't actually happen. On the contrary, being primed with an incongruent odour apparently impaired *E. culicivora*'s ability to find cryptic odour while in the olfactometer. It suggests that when *E. culicivora* is faced with a challenging task, its poor little brain has trouble coping with any more than what it was primed with!

Discovering that *E. culicivora* is attracted to the odour of *L. camara* (Chapter 6) was, of course, a critical step in designing the experiment on olfactory search images. To make the prey and mate odour sources cryptic, I needed to use a masking odour that was relevant to *E. culicivora*, and *L. camara* provided the important key, being a highly aromatic plant in *E. culicivora*'s habitat. *E. culicivora*'s affinity for all these different odour sources certainly made it a good candidate for exploring olfactory search images!

However, I'm still left with a sense that we've only just started to scratch the surface and that more should still be investigated in this area with *E. culicivora*. For one thing, I know that *E. culicivora* sometimes responds to different odour sources by performing courtship displays (Chapter 7), and I have felt for a while that it would be interesting to investigate whether being primed with a particular odour source (such as the odour of a potential mate) might trigger courtship display even in the presence of masked odour. In the experiment of Chapter 12, it was rare for individuals to display while in the olfactometer, but I kept thinking that evidence of *E. culicivora* displaying

when presented with particular, masked, odour would be more analogous to a sniffer dog starting to bark when it detects the odour of a particular drug (i.e., *E. culicivora*'s displays would be like the sniffer dog's barking). In Chapter 7, I never got the majority of the tested individuals of *E. culicivora* to display in response to odour alone but, if I follow my own advice (from Chapter 1), even if it is difficult doesn't mean it's impossible. Perhaps the next step is to try sequential priming. Or perhaps more males would display in the presence of masked odour if I could find a more effective way of strengthening the odour.

Crossing the finishing line

I have had the honour of watching a fascinating spider story unfold before me. *Evarcha culicivora* might be small, but its ability to use selective attention is no short of astonishing, using either vision or olfaction in remarkable ways for finding prey or mates, with these two parts of the spider's life seeming to converge in surprising ways. For *E. culicivora*, vision and olfaction can even work together (and in either direction) for finding blood-carrying mosquitoes. And, as if that weren't enough, *E. culicivora* also has an interesting association with two plant species which is something quite unexpected for a salticid. In fact, and I may be biased here, but much of the work in this thesis suggests that *E. culicivora* is a cut above the rest, both in comparison with other salticids and with animals in general.

So here it is, a thesis consisting of 13 chapters, but representing only one (unique) chapter of my life. And regardless of where I end up in life, I will think about this little animal that helped change my perception of the world. Of course, I

still like big animals: horses, elephants, dogs, hyraxes. But through *E. culicivora*, I went to a faraway land and learned what even a small brain is capable of doing. And yet I have a sneaky suspicion that there is a whole lot more to come. *E. culicivora* may have a small brain, but what this spider can teach us, both now and in the future, is anything but boring.

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Appendix One

From eight-legged automatons to thinking spiders

Hyrax at Hell's Gate National Park. Rift Valley, Kenya

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Chapter 9: From eight-legged automatons to thinking spiders

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Introduction

There may be compelling reasons for the traditional portrayal of spiders as simple, instinct-driven animals (Bristowe, 1958; Savory, 1928), and the very notion of *spider minds* might seem comical, if not scientifically disreputable. Of course, it depends on what we mean by minds. Instead of formally defining *mind*, we could accept that "minds are simply what brains do" (Minsky, 1986). Yet the idea that *spider minds are what spider brains do* may sound too flippant. Minksy must have been thinking about *real* brains (i.e., big brains, especially human brains). After all, how much can the minute brain of a spider do? Being so small and primitive, aren't spiders just eight-legged automatons?

Minsky's catchy phrase is not so much a definition but instead something more like a decision to refrain from proposing a formal definition, and a radical departure from Descartes' (1637/1994) ontological distinction between mind and matter. The Cartesian Dichotomy has been almost like a philosopher's no-trespassing sign telling scientists to keep out (i.e., philosophers may have the *problem of the mind*, and it just isn't a scientific problem).

"What brains do" is accessible to scientific investigation, but there is still a lingering feeling that the mind cannot be everything that brains do. We can envisage an animal as receiving a stimulus and orchestrating a response, with the brain doing something we call *information processing* in between. Mind might seem more appropriate for especially intricate information processing. On the other hand, when information processing is not

especially intricate, then *automaton* may seem to be a more appropriate term. However, looking for a sharp boundary between the two may be counterproductive.

Yet there may be a feeling that words such as *intricate* and *elaborate* are inadequate for what mind is about. In philosophy, the mind is traditionally envisaged as having three faculties (Allen, 1952; Hilgard, 1980; LeDoux, 2002; Plato, 1964; Tallon, 1997), *thinking* (cognition), *feeling* (emotion) and *wanting* (volition), with the connotation of automaton being an entity with behaviour but none of these underlying faculties.

Attention is another attribute traditionally affiliated with cognition, and contrasted with *automatic*. Despite William James' (1890) suggestion that "everybody knows what attention is", modern cognitive psychologists are more inclined to say the opposite, that "no one knows" (Pashler, 1998). Yet issues related to selective attention may be pivotal for understanding the behaviour of some of the animals traditionally envisaged as automatons. In this chapter, we illustrate this by considering recent work on some particularly unusual spiders, namely, species that specialize at eating other spiders and species that specialize at drinking vertebrate blood.

Search Images

Understandably, research on attention, like most cognition research, has been driven primarily by an interest in a particular animal species, *Homo sapiens*. However, independent of the human-oriented psychological tradition, biologists who study the behaviour of non-human animals have also grappled with the topic of attention, but largely by another name, *search images*. This topic is usually traced back to Lukas Tinbergen. The name Tinbergen is, of course, strongly associated with research on animal behaviour, with Niko Tinbergen being widely regarded as one of the founders of ethology (Kruuk, 2003). Lukas and Niko Tinbergen were brothers, but Lukas was primarily an ecologist, not an ethologist. His remarkable field-based research on insectivorous birds in the Netherlands began in 1946 and ended with his untimely death in 1955 at the age of 39 (Baerends & de Ruiter, 1960). Five years later, his work was published posthumously (Tinbergen, 1960), and his hypothesis that birds adopt search images was presented in this paper. His original term was *searching image*, but now this is usually shortened to search image. The rationale for Tinbergen's hypothesis arose from comparing the relative abundance of different types of insects in a bird's diet with the abundance of different types of insects in the same habitat. He envisaged search images as

perceptual changes, the idea being that the predator, after discovering a particular type of prey, *gets an eye for* or *learns to see* this particular type of prey.

Tinbergen (1960) also suggested that predators "perform a highly selective sieving operation on the visual stimuli reaching their retina" (p. 332). *Sieving*, or *filtering*, implies that certain features of the prey are ignored, whereas other, more salient features are attended to. Humans have shown evidence of sieving through visual-search paradigms, where a particular target with a certain configuration of features is searched for within a crowd of distractors lacking in this configuration (Pashler, 1998; Treisman, 1986; Treisman & Gelade, 1980). Reading Tinbergen's paper now, more than 40 years later, is an uncanny experience. Here was a field biologist coming to grips with the cognitive implications of animal behaviour while writing for what appears to be primarily an audience of ecologists. *Ahead of his time* seems like an understatement (see Wasserman, 1997).

Tinbergen lived in a time when Behaviourism ruled in comparative psychology, and animal cognition was almost never talked about, even by psychologists. A term like *attentional priming* would have been unfamiliar to Tinbergen. However, it is clear that what he meant by learning to see was that previous experience by the predator with a particular type of prey primes the predator to be selectively attentive to specific features of this particular prey (see P. M. Blough, 1989, 1991, 1992; Brodbeck, 1997; M. Dawkins 1971a, 1971b; Langley, 1996; Langley, Riley, Bond, & Goel, 1996; Reid & Shettleworth, 1992).

Tinbergen's search-image hypothesis was the impetus for numerous studies undertaken over the last four decades, especially ones using birds as the subjects (Bond & Kamil, 2002; Croze, 1970; Lawrence, 1986; Mook, Mook, & Heikens, 1960). However, it has also been the source of considerable controversy (Guilford & M. Dawkins, 1987; Lawrence & Allen, 1983). Although some authors have clearly appreciated that Tinbergen's hypothesis was about the priming of selective attention (e.g., Bond & Kamil, 2002), attention and priming are not routine concepts in ecology. Yet it was especially for ecologists that Tinbergen was writing and it is especially in ecology that the term search image came to be frequently used, and misused. As we discuss later (see section on Preferences), perhaps the most common misuse has been to blur the distinction between demonstrating that a predator develops preferences for particular kinds of prey and demonstrating that predators adopt search images (e.g., Morgan & Brown, 1996). M. Dawkins (1971a) concluded that we should abandon the term search image altogether because its meaning has been so badly eroded by misuse, but we should not surrender this interesting term. It speaks for itself, triggering

associations with issues that are clearly cognitive. In particular, *image* sounds like *imagery*, and imagery at its core pertains to cognition (Neiworth & Rilling, 1987).

Perhaps, for many scientists during the four decades following Tinbergen's paper, the literal interpretation of imagery as a picture in the animal's mind was too incompatible with prevalent views in comparative psychology, ethology and behavioural ecology. An alternative word is *template*, and there is a tradition of using this term in animal studies, with the best known examples perhaps being from research on the ontogeny of bird song (Catchpole & Slater, 1995; Konishi, 1964, 1965; Konishi & Nottebohm, 1969; Marler, 1952). The term template is also used in research on kin recognition (Waldman, Frumhoff, & Sherman, 1988) and landmark-based navigation (Collett, 1995; Schuster & Amtsfeld, 2002).

It has also been adopted in cognitive research on humans (e.g. Neisser, 1967), although it has often been criticized for suggesting something too simplistic (Palmer, 1999). However, simplistic interpretations can be valuable because they guide the direction of our thinking while we strive to derive more realistic models. Search-image use might be interpreted as the predator having a mental template (a representation of what a particular kind of prey looks like) against which it compares what it sees when searching for prey (Anderson, 2000; Reid & Shettleworth, 1992). Image and template both emphasize the predator's ability to detect and identify prey.

High-Acuity Vision With Minute Eyes

It is not surprising that most of the literature on search images concerns the priming of visual attention. People can see exceptionally well, and it is easy for us to relate to other animals that also see well. On the other hand, most spiders have poorly developed eyesight (Homann, 1971; Land & Nilsson, 2002), which may discourage search-image studies on these animals. There is, however, a distinctive exception. Jumping spiders (Salticidae) have unique, complex eyes (with an acuity of 0.04°; Blest, O'Carroll, & Carter, 1990; Blest & Price, 1984; Williams & McIntyre, 1980) that support spatial resolution ability unparalleled by other animals of comparable size (Land & Nilsson). Their acuity actually exceeds that of some of the *conventional* subjects of search-image research (see Harland, Jackson, & Macnab, 1999). Among insects, the highest acuity (0.4°) is found in a large dragonfly, *Sympetrum striolatus* (Labhart & Nilsson, 1995). Our acuity is 0.007° (Kirschfeld, 1976), only five times better than a salticid's (Figure 1).

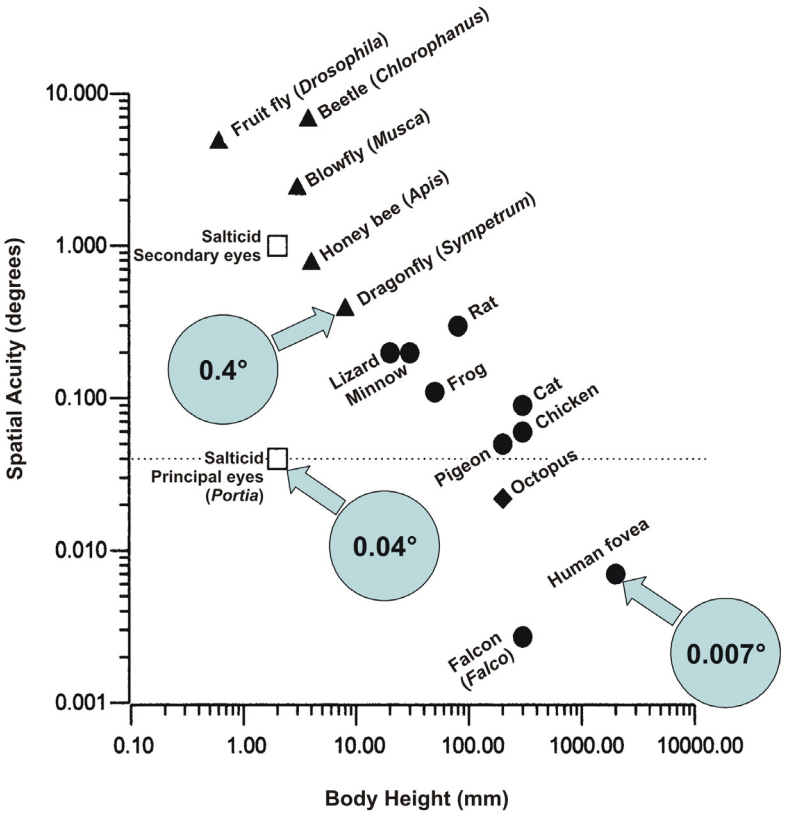

Figure 1. Spatial acuity of *Portia*'s eyes compared with eyes of other animals. The log of spatial acuity is plotted against the log of body height. Triangles: insect compound eyes. Squares: salticid eyes. Circles: vertebrate eyes. Diamond: cephalopod eyes. Modified after Harland & Jackson (2004). Data from Kirschfeld (1976), Land (1985, 1997) and Snyder & Miller (1978).

Adults of most salticids are less than 10 mm in body length, and these small spiders are easy to identify. Stare at a spider. If it stares back with big forward-facing principal eyes (Figure 2), then it is a salticid. Salticids actually have eight eyes, six of which (the *secondary eyes*) are positioned around the side of the carapace and function primarily as motion detectors (Land, 1971). It is the forward-facing *principal eyes* that process details about the objects being viewed.

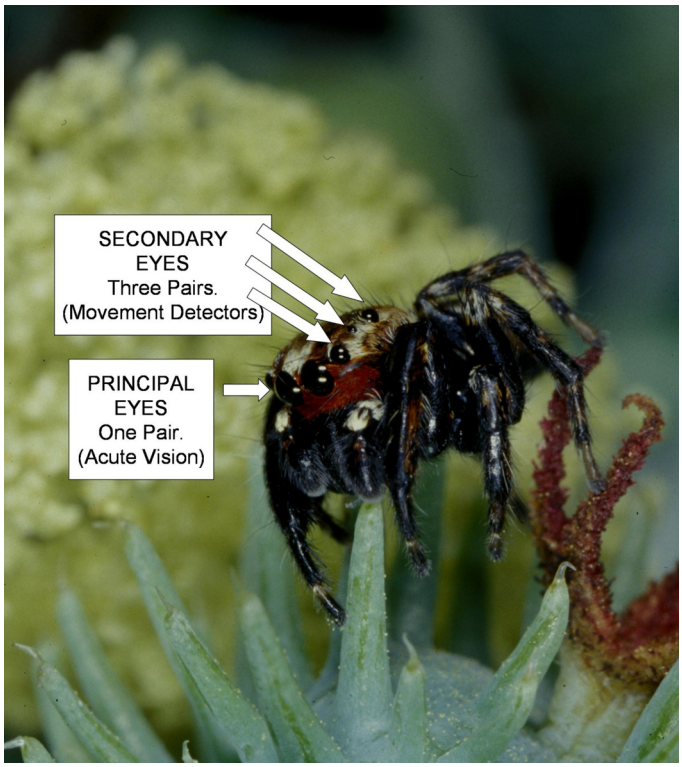

Figure 2. Adult male of *E. culicivora* with principal and secondary eyes indicated.

The salticid's principal eyes are large by spider standards, but the human eye is much bigger. Conventional wisdom dictates that seeing fine detail requires a big eye, but defying conventional wisdom seems to be a salticid specialty. Our retinae contain about 130 million photocells (Palmer, 1999), quite unlike the salticid eye which has photocells numbering only in the thousands (Land, 1969b). Like the human retina, the salticid's principal-eye retina has a fovea (Blest et al., 1990), a region where receptor spacing is optimal for image resolution when using light in the visual spectrum. However, the human fovea has millions of receptors, whereas the salticid fovea has, at most, about 200 (Blest et al.). If for no other reason, small animals should not see especially fine detail simply because big eyes will not fit on a small body.

The problem with small eyes also applies to small brains. There is more to seeing than what meets the eye. That is, seeing is also the product of cognitive processes (Barry, 1997; D. S. Blough & P. M. Blough, 1997; Palmer, 1999; Schiffman, 1996; Shettleworth, 1998), and the number of neurons in the salticid's brain is minute compared with the human brain (Harland & Jackson, 2000). Smaller animals tend to have fewer, not smaller, neurons (Alloway, 1972; Bullock & Horridge, 1965), which means that smaller animals have fewer components for their brains and sense organs, the machinery used for collecting and processing information. We expect big brains to have greater potential for performing

complex tasks (e.g., visual attention tasks), whereas the salticid brain is small enough to fit on a pinhead (Harland & Jackson, 2000). We have to wonder what tasks salticids can actually perform, especially when we consider that even in much larger animals it is widely held that brain size limits cognitive ability (Lashley, 1949; Maunsell, 1995; Rensch, 1956). However, salticids have a way of surprising the sceptic. Future research should carefully consider potential relationships between behaviour complexity and details of salticid brain morphology, as well as ratios of brain weight to body weight (see Meyer, Schlesinger, Poehling, & Ruge, 1984).

Predatory behaviour reveals what seeing detail means for a salticid. Most salticids are more or less generalist predators of insects (Richman & Jackson, 1992). However, there are some pronounced examples of salticids that have specialized preferences and exhibit prey-specific prey-capture behaviour. In particular, *Portia* is a genus of primarily tropical salticids from Africa, Asia and Australia that specialize at eating other spiders and *E. culicivora* is an East African salticid that specializes at indirectly feeding on vertebrate blood by selecting blood-fed mosquitoes as prey. *Portia* adopts different tactics for capturing different kinds of spiders. These include different tactics for different species of spider prey, and even for different individuals of a single species of spider prey. Within-species distinctions include whether the prey spider is carrying eggs or not (Li & Jackson, 2003). *E. culicivora* distinguishes between mosquitoes and midges that are similar in size and appearance. It also distinguishes between female and male mosquitoes and between female mosquitoes that have recently been feeding on blood and those that have not (Jackson, Nelson & Sune, 2005). It even distinguishes between blood-fed females belonging to different genera of mosquitoes (Figure 3). The spider-eating and mosquito-eating salticids have been shown experimentally to make these discriminations by sight alone, with prey shape being especially salient to the salticid. Evidence for this includes testing the salticids with projected computer-generated animation (Harland & Jackson, 2002; Pollard, 2004). These examples highlight the challenge for any attempt to understand salticid vision. How can they do so much with so little?

Figure 3. Adult male of *E. culicivora* eating *Anopheles gambiae*, the mosquito species that is the primary vector of malaria in Africa.

Salticids, like vertebrates, have camera eyes, instead of compound eyes, but salticid and vertebrate eyes function very differently (Land, 1974). Light enters through the corneal lens (Figure 4), which is fixed in place on the spider's cuticle, and passes through a long, narrow eye tube and then, at the rear of the eye tube, goes through a second lens that magnifies the image (Williams & McIntyre, 1980). Light next passes through a complex retina. Unlike the human eye, which has a retina on a single plane, the salticid retina consists of four layers, and light passes successively through each layer. The tiered arrangement of the salticid's retina is important for colour vision because the retina takes advantage of how the lens system causes chromatic aberrations (i.e., different wavelengths of light are diffracted differently by the lens and come into focus at different distances, corresponding with layers II–IV of the retina; Blest, Hardie, McIntyre, & Williams, 1981; Land, 1969b).

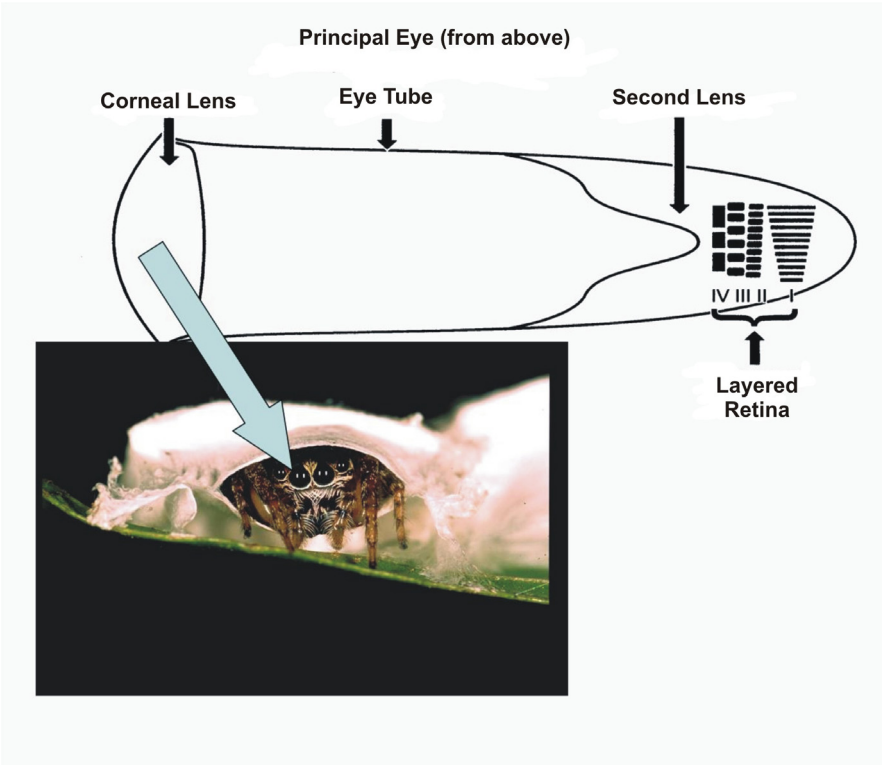

Figure 4. Salticid principal eye. Drawing by D. P. Harland.

Within layer I of the principal-eye retina, there is an additional structural detail, a staircase arrangement of the receptors that functions in focussing (Blest et al., 1990). There are six muscles attached to each eye tube, but these muscles do not effect changes in shape (i.e., unlike our eye, the salticid eye cannot focus by accommodation). These muscles are important for focussing, however, because they sweep the retina across the image projected by the corneal lens. At any distance away from the eye, the image falls on some portion of the staircase during these side-to-side sweeps.

The fovea is in the central region of the staircase and the eye-tube muscles organize other, more intricate movement patterns, including saccades and tracking, and especially scanning (Land, 1969a). When the image of an object of interest has been fixated upon, the eye tube scans by rotating while simultaneously moving side to side. Scanning may be a method by which the salticid actively searches for lines or other salient features on the image in its visual field (Harland & Jackson, 2000; Land 1969a). Actively piecing together a scanned-in picture of the viewed object may be the salticid's solution to the problem of how to discern detail using a fovea containing only about 200 receptors.

Much as we may be tempted to praise our favourite spiders, part of what it means to say an animal sees well should perhaps be that it perceives what is out there quickly. On this

criterion, salticids may see only poorly (Harland & Jackson, 2000). Although *Portia* discriminates accurately between different kinds of spider prey and *E. culicivora* discriminates accurately between blood-fed and sugar-fed female mosquitoes, it is routine for *Portia* and *E. culicivora* to stare at potential prey for many minutes before responding. Discriminations that are more accurate tend to follow these long bouts of preliminary staring, and those that are less accurate are typical when the salticid hurries (Figure 5).

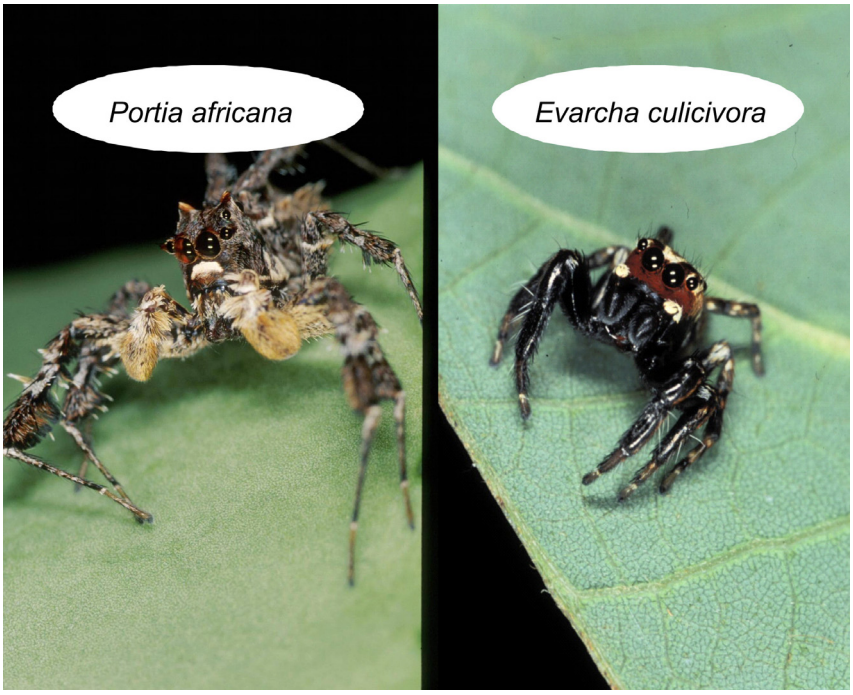

Figure 5. Salticids that make especially fine distinctions between different kinds of prey. *Portia africana*: distinguishes by sight between different species of other spiders on which it preys. *Evarcha culicivora*: feeds indirectly on human blood by selecting as prey female mosquitoes that have had recent blood meals. Although they make these distinctions, it may take a long time for them to do it.

Capacity Limits

In research on attention, constraints on cognitive ability are usually attributed to *capacity limitations*. *Capacity* can be thought of as a perceptual resource that is used during the performance of a given task or process and how much of this resource is available to an individual may vary depending on various factors, including motivation, alertness and time of day (Kahneman, 1973; Palmer, 1999).

Attention is a field where research on vertebrates, especially humans, predominates (Pashler, 1998), and capacity limitations on selective-attention tasks are evident even in these large animals (Desimone, 1998; Dukas & Kamil, 2000, 2001; Rees, Frith, & Lavie, 1997).

Although Tinbergen (1960) suggested that birds might use more than one search image at a time, later research suggested that, even in vertebrates, being selectively attentive to one prey type interferes with detecting other types (Bond, 1983; Pietrewicz & Kamil, 1979). With the current convention being to envisage large animals as constrained to adopt only one search image at a time, it is not surprising that small animals, such as salticids, are only used rarely as subjects in search-image studies. Whether a spider-size brain can mobilize the cognitive capacity required for search images at all might appear debatable.

Spatial proximity between objects and the information load on the perceptual system are two different issues that have been regarded as primary influences on human visual attention. *Spotlight* and *zoom lens* have been commonly used as metaphors in literature that emphasize the importance of spatial proximity. According to the spotlight model, attention focuses on a certain region of the visual field (i.e., the region is *illuminated*), so that objects in this region mentally stand out from objects in less illuminated regions. Once the objects in the illuminated region have been processed, the spotlight moves to another region of the visual field and in this way successively more objects are processed (B. A. Eriksen & C. W. Eriksen, 1974). However, it has been argued that the spotlight is not fixed in size, but more like a zoom lens that can be widened or narrowed, depending on the task (e.g. Palmer, 1999). According to the zoom-lens model, visual processing is faster when attention is concentrated in a small visual field, but slows as this attended visual field expands (C. W. Eriksen & St. James, 1986). As the attended visual field expands, specific details of objects in the field become less distinctive, meaning that these objects (both targets and distractors) are more difficult to process.

Lavie's perceptual-load model (Lavie, 1995; Lavie & Tsal, 1994) emphasizes the role of information, rather than spatial proximity, arguing that visual processing is automatic, but with processing being focussed on relevant, before irrelevant, items. According to this model, a low load (e.g., a task requiring the viewing of only a few objects) is easy to process and, therefore, resources are used in processing not only the target but also at least some of the distractors (i.e., after processing the target, the excess capacity that has been left over is used to process the distractors). However, when the perceptual load is high (e.g., when a task requires the viewing of many objects at once), Lavie's hypothesis predicts that few, if any, distractors will be processed because resources have been used up in processing the target.

In work on human attention, no clear consensus has emerged favouring any one of these models—spotlight, zoom lens or perceptual load (see Chen, 2003). This is potentially an area where animal-based, and even spider-based, research on search-image use will be

especially instructive (see Vreven & P. M. Blough, 1998). At first glance, both spatial proximity and information load appear to be particularly relevant to understanding visual attention in salticids. In the literature on large vertebrate eyes, it is routine to point out that gaze and attention are two different things (Palmer, 1999). However, for a salticid, gaze and attention might be more tightly linked. This would be particularly true if, as proposed (Harland & Jackson, 2000; Land 1969b), scanning routines directed at small areas in a much larger image are an integral part of the processing of visual information by the salticid's principal eye retina. A scanned region of an image suggests the spotlight metaphor. The zoom-lens metaphor is not so clearly applicable.

The perceptual load model also appears, at first glance, to be highly relevant because of conventional wisdom that small nervous systems are especially limited in capacity. Excess capacity, left over after processing targets, might be considerably less evident in a salticid than in a much larger animal such as a bird or a primate.

How Salticids Use Search Images

Paraphrasing Ware (1971), Lawrence (1986) predicted that "future work on the relation of learning to feeding behaviour will undoubtedly reveal that the development of a search image is an extremely complex process but is likely to be a fundamental characteristic of vertebrate predation" (p. 11). There are two ways in which recent findings from research on salticid spiders are at odds with Lawrence's statement. Salticids are not vertebrates, and the salticid work questions whether the emphasis on learning in the search-image literature is necessary. Typically, search-image studies are carried out by repeatedly exposing the predator to a particular prey type, eventually resulting in selective visual attention by the predator to this prey type being primed (Gendron, 1986; Gendron & Staddon, 1983; Royama, 1970). This is consistent with the hypothesis that search images are acquired by perceptual learning.

Evidence of search-image use by a salticid comes from two experiments using *Portia labiata* from Los Banos in the Philippines and three prey species (Jackson & Li, 2004). The individuals of *Portia* that were used had no prior experience with any of these three prey species. *Portia* is known to have an active preference for spiders as prey (Jackson & Pollard, 1996; Jackson & Wilcox, 1998) and, while it also eats insects, insects are not its preferred prey. Two of the prey species in the search-image study were common spiders on which *Portia* preys in nature (preferred prey), and the other prey (non-preferred) was the common house fly, *Musca domestica*. The individuals of *Portia* used in the study were reared in the

laboratory and had no prior experience with any of these three prey species. At least for people, the two prey spiders, *Scytodes pallida* (Figure 6) and *Micromerys* sp. (Figure 7), were distinctly different in appearance. *S. pallida* is a spitting spider (Scytodidae) with a characteristic heavy-set appearance. *Micromerys* sp. is a pholcid spider with a slender, pencil-like body and characteristic long legs. In each instance, *Portia* was given the opportunity to capture and eat one of the two types of spiders or a fly. *Portia* was then given access to combinations of prey. Depending on the experiment, the spiders and flies were either alive or they were lures (dead prey mounted in lifelike posture on cork disks). The experiments revealed no evident effect of prior experience with a house fly. However, during testing, *Portia* found *S. pallida* more often when initially allowed to eat *S. pallida*, and found *Micromerys* sp. more often when initially allowed to eat *Micromerys* sp. Moreover, *Portia* found *S. pallida* less often after initially eating *Micromerys* sp. and found *Micromerys* sp. less often after initially eating *S. pallida*. *Portia*'s ability to find a previously encountered prey spider, but not a fly, suggests that the predator has an innate predisposition to adopt search images for particular types of prey from the preferred category (i.e., spiders).

Figure 6. Portia labiata (left) from the Philippines stalking a spitting spider, *Scytodes pallida* (right). Having executed a planned detour, *P. labiata* approaches from the rear (i.e., *S. pallida* is facing away from *P. labiata*), away from *S. pallida*'s line of fire.

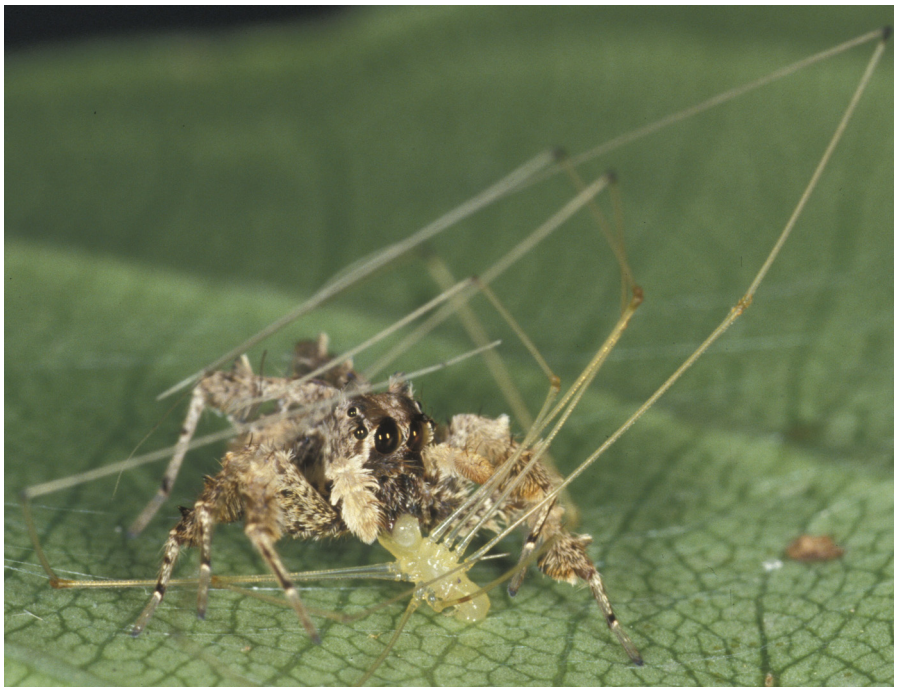

Figure 7. Portia labiata eating *Micromerys* sp., a pholcid spider from the Philippines.

When lures instead of living spiders were used, one of the variables was whether or not the prey was partially hidden from the predator's view. When not partially hidden, there was no evidence that detection of either type of spider prey was influenced by *Portia*'s previous meal (Jackson & Li, 2004), which suggests that *Portia*'s adoption of search images becomes detectable only when the prey is difficult to see (*crypticity*). This can be interpreted as prey on a cryptic background presenting *Portia* with a high perceptual load (i.e., the features of the background were, for *Portia*, distracting, and this increased the load on *Portia*'s perceptual system). Continuing with this interpretation, having a search image may have enabled *Portia* to be efficient at identifying the prey type for which it was prepared, but left with insufficient resources for efficiently identifying the other prey (i.e., for identifying the prey for which *Portia* was not prepared with a search image). When the prey was not cryptic, being prepared with a search image mattered less because the perceptual load was less and *Portia* could identify efficiently even the prey for which it was not prepared.

One-encounter search-image adoption has actually been shown before. Rattlesnakes form chemical search images for particular prey items immediately after striking these prey (Melcer & Chiszar, 1989). Perhaps the snake and spider learn what the prototypical prey type looks or smells like after a single exposure, but an alternative hypothesis is that exposure to a particular type of prey calls up an innate template.

Cross-Modality Priming

Search-image research has generally focussed on one sensory modality at a time (i.e., a typical search-image hypothesis is that prior experience with a visual cue primes attention to this same visual cue). However, recent cognitive research has highlighted that a cue in one modality (e.g., olfaction) may cause attentional changes in another modality (e.g., vision). This is known as cross-modality priming. For example, cross-modality priming might occur when detecting a particular odour cue from a particular prey item prepares an animal for detecting a particular visual cue from the same prey item. So far, little is known about cross-modality priming in humans (Driver & Spence, 1998; Pauli, Bourne, Diekmann, & Birbaumer, 1999; Stein, Wallace, & Stanford, 2001) or other animals (Martin-Malivel & Fagot, 2001). However, recent research on predatory behaviour suggests that cross-modality priming may be prevalent in *Portia* and other salticids (Clark, Jackson, & Cutler, 2000; Jackson, Clark, & Harland, 2002).

For *Portia fimbriata* from Queensland (Jackson et al., 2002), cross-modality priming assists in the capture of a particular prey species, namely, *Jacksonoides queenslandicus*, another salticid that is commonly found in the same habitat (Figure 8). *J. queenslandicus*' odour primes selective attention by *P. fimbriata* to optical cues from specifically *J. queenslandicus* (i.e., the smell of *J. queenslandicus* prepares *P. fimbriata* to see specifically *J. queenslandicus*). Something similar has recently been found for *E. culicivora*: odour from female mosquitoes that have recently fed on blood prepares *E. culicivora* to see specifically blood-fed female mosquitoes (unpublished data). As in the search-image study (Jackson & Li, 2004), the individuals of *Portia* and *E. culicivora* used in the cross-modality priming studies had no prior experience with the prey species used in the experiments.

Figure 8. Portia fimbriata from Queensland eating *Jacksonoides queenslandicus*. *J. queenslandicus*, like *P. fimbriata*, is a salticid and has acute vision. Odour from *J. queenslandicus* prepares *P. fimbriata* to see *J. queenslandicus* before seen by *J. queenslandicus.*

When interpreting the findings from the search image experiments, it seems appropriate to ask how a single experience of seeing a particular prey's features influences the same predator to selectively attend to these same features at a later time. However, this question is not applicable when interpreting the findings from the cross-modality priming studies. Here, individuals of the predator, *P. fimbriata* or *E. culicivora*, became selectively attentive to the appearance of the prey type, *J. queenslandicus* or a blood-fed mosquito, after being exposed to the prey's odour (i.e., a specific odour, not appearance, evidently triggered selective attention to specific features of appearance). A metaphor for this might be that the odour of a particular prey type called up a pre-formed search image (i.e., a disposition for selective visual attention to features of this prey type's appearance). Something similar should be considered for the findings from the more conventional search image study (Jackson & Li, 2004). Perhaps, for *Portia labiata*, a single prior experience of seeing *Micromerys* or *Scytodes* called up an innate pre-formed disposition for selective attention to features of *Micromerys* or *Scytodes*, respectively. *P. labiata* may be equipped with innate search images for some of its more preferred prey (spiders), but not for less preferred prey (insects).

Preference

In behavioural ecology, there has been a long tradition of making casual use of terms such as *prefer, want, choose* and *decide,* often with an explicit disclaimer of any cognitive implication being intended. As an effective writing ploy, there is nothing particularly objectionable about using cognitively-loaded words in a non-cognitive context, so long as we can reclaim these words when we need them for making distinctions that actually are related to cognition. One word we need to reclaim is *preference*. Diluted use of this term has become habitual in ecology and this diluted use has probably been largely responsible for the erosion of Tinbergen's original meaning of search image.

It has become commonplace in ecology to equate a predator's diet, choice and preference (e.g., Manly, 1974; Roa, 1992). For example, Lockwood's (1998) view was that "the relative consumptions of different food types" corresponds closely "with our intuitive definition of "preference"" (p. 476). Perhaps what is *intuitive* in ecology is different, but our intuition is that an animal's preference is what it would like to eat and that this allows for the possibility of an animal's diet (what it actually does eat) being different from its preferences. A predator's diet must often be influenced by things that do not intuitively correspond to the notion of what the animal wants. An obvious example is the prey animal's defences against the predator. Maybe the predator can't always get what it wants. Preference is an appropriate word for the predator's attitude toward different types of prey and *choice* is an appropriate word for behaviour and more specifically a type of behaviour that is driven by preference. Diet may suggest hypotheses about preference and these hypotheses may predict the choices a predator will make in experiments, but data on diet alone do not simply reveal a predator's choices and preferences.

Tinbergen's data came from sampling in the field, not from experimentation. His data revealed biases in the diets of predators in the field (i.e., diet deviated in particular ways from the relative abundance of the different potential prey types in the field). One of the more interesting and useful things Tinbergen did was to derive an innovative hypothesis concerning the determinants of the trends he found by sampling. Search-image use was his hypothesis, not his findings. No amount of sampling of the type he did could ever simply demonstrate that animals adopt search images. Experimental studies of behaviour are required for that.

Ecologists have a habit of using the word preference for what an animal eats, rather than for one of the potential reasons why it might eat what it eats. This has led to the

misleading tendency to equate the notion of a predator adopting a search image for a particular prey type with the notion of a predator adopting a preference for this prey type. This misses the point about search images. Search-image use is, as a determinant of diet, an alternative to preference. Preference is expressed by choice behaviour, whereas search images are shifts in selective attention. The two are not the same, and this is why most of the literature emphasizes that search-image use is expected to be relevant primarily when prey are cryptic.

Specialization

Our research on salticid predatory behaviour has sensitized us not only to the terms search image and preference, but also to the term *specialization*. *Portia* and *E. culicivora* are specialized in the literal sense of doing something special, but it is the particular ways in which they are special that is of interest. Just saying they are specialists does not get us very far.

Diet is a good place to start. In the field, *Portia* eats lots of spiders and *E. culicivora* eats lots of mosquitoes, and these are unusual (*special*) biases in their diets. Few salticids appear to prey so often specifically on other spiders or specifically on mosquitoes. *Portia* and *E. culicivora* also execute different prey-specific prey-capture behaviour patterns in their encounters with different types of prey (i.e., the behaviour they adopt during encounters with different kinds of prey are special to those kinds of prey). Curio (1976) called the use of multiple prey-specific prey-capture tactics *predatory versatility*, but the term *conditional predatory strategy* (R. Dawkins, 1980; Dominey, 1984) seems to be more widely used now. Predatory versatility is especially pronounced in *Portia*. Each individual of *Portia* has a repertoire of many different prey-capture tactics, and rules for when to use these different tactics.

Portia and *E. culicivora* are specialized in yet another way. These predators make unusual prey-choice decisions that evidently reveal specialized preferences. The tradition in behavioural ecology notwithstanding, understanding these predators requires that we reclaim the word preference and apply it as a cognitive attribute of the predator rather than using it simply for what the predator eats. Prey-choice behaviour is an appropriate term specifically for situations where we have evidence that a predator distinguishes between different types of prey and then attacks (i.e., chooses) one rather than the other (see Fox & Morrow, 1981; Morse, 1980). In the Canterbury Spider Laboratory, we do extensive research on the prey-

choice behaviour of salticids, this work being designed specifically to rule out many of the factors other than preference that might determine diet. In particular, by testing with stationary lures instead of living prey, we remove variables such as prey defence when considering potential influences on test outcome. These laboratory experiments have provided us with extensive evidence that *Portia* and *E. culicivora* do indeed perceive differences between different types of prey and decide to attack one instead of the other.

Representation

Using the term search image suggests something like a picture of a prey item being held in the animal's mind. *Image* in *search image* suggests imagery. Proposing that encounters with prey alter a spider's brain, calling into play mechanisms for selective attention somehow sounds less provocative than the notion of a mental picture. *Mind pictures* are better known by cognitive psychologists as *representations* (e.g. Palmer, 1999), and a number of search-image researchers have interpreted findings from search-image studies as evidence that predators make use of representations (e.g. Endler, 1988; Pietrewicz & Kamil, 1981). Representation is often envisaged as a key attribute that more or less defines the boundary between what does and does not qualify as cognition (e.g., Damasio, 1994).

Part of the excitement research on search-image use by salticids generates comes from appreciating that even an animal so small may be a useful model for studying representation. Interestingly, there are yet other findings from research on salticids that appear to be relevant to understanding representation. *Portia*'s use of detours is an example. A simple definition of a detour is an indirect path to a target, and there has been a long tradition of testing the abilities of mammals to reach targets by taking deliberate detours (Chapuis, 1987; Guillaume & Meyerson, 1930; Thorndike, 1911; Wyrwicks, 1959).

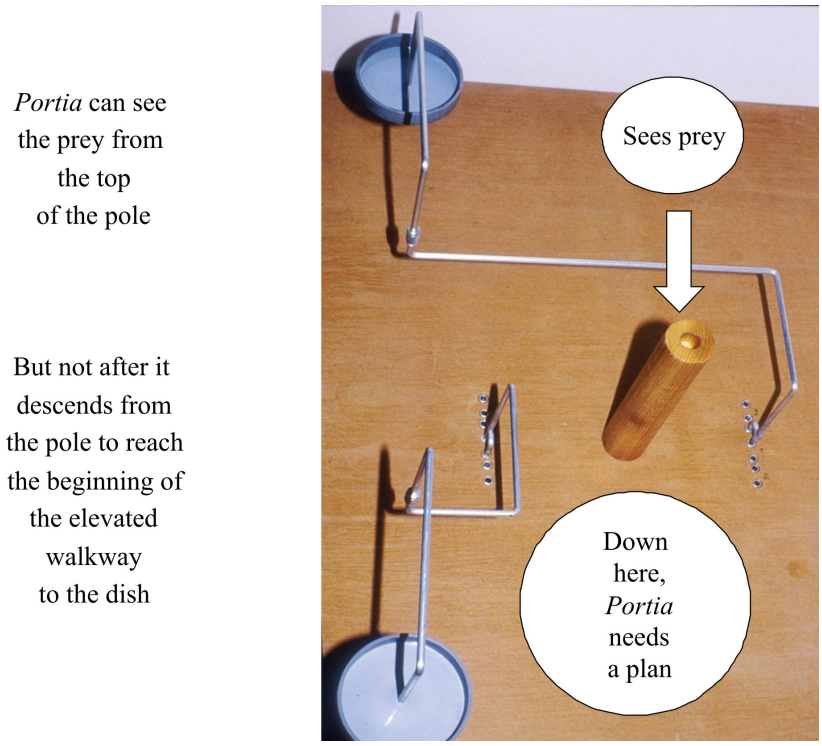

Figure 9. Apparatus used for testing ability of *Portia fimbriata* to plan detours. *Portia* on top of pole in centre before testing begins. Prey item (lure made by mounting dead spider in lifelike posture on cork disk) (not shown) in one of two dishes (whether on left or right decided at random). *Portia* views prey while on top of pole, but cannot see prey when goes down pole (i.e., reaching prey consistently depends on *Portia* planning route before leaving pole).

In the field *Portia* readily takes detours that enable it to reach advantageous positions from which to attack its prey (Jackson & Wilcox, 1998). Findings from numerous experimental studies in the laboratory imply that *Portia* actively chooses its route to a target (Tarsitano & Andrew, 1999; Tarsitano & Jackson, 1997). One set of experiments (Tarsitano & Jackson) presented *Portia* with a choice of two convoluted routes (Figure 9), only one of which led to the target (a lure made by mounting a dead spider in lifelike posture on a cork disk). *Portia* could see the target and the lay-out of the two paths at the beginning of a trial, but not once it walked away, with the rationale for this testing design being to force *Portia* to plan ahead. Sometimes *Portia* had to walk past the entry into the incorrect route before reaching the entry into the correct route. Sometimes taking the correct route required initially moving directly away from the lure, and sometimes the correct route was considerably longer than the incorrect route. Yet, regardless of layout, *Portia* took the correct route significantly more often than the incorrect route. These findings suggest that, while at the starting position, *Portia* acquired a representation of one of the two routes leading to the lure and that *Portia*

used this representation while the lure was out of sight. Salticid spiders may be small, but their cognitive abilities may not be as limited as one might think.

Summary

Over 40 years ago, Lukas Tinbergen proposed a provocative hypothesis, that predators adopt search images for particular kinds of prey. The idea with search images is that a predator is primed by prior exposure to a particular type of prey, and becomes selectively attentive to cues from that prey. Although the cognitive implications of this hypothesis were initially greeted with controversy, a later tradition emerged in the ecological literature of blurring the distinction between selective attention and preference. The controversy appeared to dissipate, but at the cost of throwing out much of what makes search images interesting. The word *image* in the term *search image* can be likened to a picture (or *representation*) in an animal's mind, with representation being a distinctively cognitive concept. Still other traditions have inhibited research on the cognitive implications of search-image use, one of these being governed by the conventional wisdom about how brain size is related to cognition. Tinbergen's research animals were birds, and he may have been ahead of his time by suggesting that interesting cognitive abilities were achievable by bird brains. In this chapter, we review recent research on the flexible behaviour of even smaller-brained animals, jumping spiders (family Salticidae). The adults of these spiders are rarely more than about 10 mm in body length, and their brains are small enough to fit on a pinhead, yet they have unique, complex eyes and eyesight that rivals a primate's. As case studies, we consider two particular examples from the salticids, namely, *Evarcha culicivora*, an East African species that specializes at feeding on vertebrate blood by preying on blood-filled female mosquitoes, and *Portia*, a genus of salticids that specializes at preying on other spiders. Priming of selective attention, search-image use and representation appear to be critical concepts for understanding recent experimental findings obtained from research on these small-brain animals.

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Appendix Two

Influence of seeing a female on the male-male interactions of a jumping spider, *Hypoblemum albovittatum*

Flamingos at Lake Nakuru National Park. Rift Valley, Kenya

Pages 290-297 of thesis.

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Influence of seeing a female on the male–male interactions of a jumping spider, Hypoblemum albovittatum

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Abstract An important prediction from game theory is that resource value influences the level to which competitors will escalate conflict. An earlier study considered whether this prediction applies to the male–male interactions of *Hypoblemum albovittatum*, a jumping spider (Salticidae) from New Zealand. The males of this species escalated conflicts in the presence of a moving mount made from a conspecific female. However, because the control was only a similar-sized motionless cork, an alternative hypothesis (that the cue for escalation is seeing movement of any female-size object, rather than seeing specifically a female) was not ruled out. Here we show that a moving cork, without a mount present, is indeed sufficient to cause males to escalate, but a moving mount (made from a conspecific female) causes males to escalate further. The level of escalation in the presence of a moving mount made from prey (housefly) or from a rival (conspecific male) did not differ significantly from the level of escalation when only a moving cork was present. These findings suggest that, although seeing a moving object similar in size to a conspecific female is sufficient for priming males to escalate, males can also discern by sight that specifically a female is present and, when they have this precise information, they make strategic decisions to escalate conflict further.

Appendix Three

Influence of optical cues from conspecific females on escalation decisions during male-male interactions of jumping spiders

Hartebeest at Nairobi National Park, Kenya

Pages 299-304 of thesis.

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Influence of optical cues from conspecific females on escalation decisions during male–male interactions of jumping spiders

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Abstract

An important prediction from game theory is that the value of a resource influences the level to which male–male conflict escalates. An earlier experimental study showed that males of *Hypoblemum albovittatum*, a common salticid in New Zealand, can discern by sight alone whether a female is in the vicinity and that, having detected a female's presence, males escalate (i.e., adopt behaviour that is likely to put them at greater risk of injury). Seeing a bare moving cork, a conspecific male or a prey item also elicits escalation, but not to the level elicited by seeing a conspecific female.

Here the earlier study is extended by using non-conspecific females in control tests and by undertaking experiments with an additional six salticid species. Findings from these experiments suggest that the ability of interacting males to detect by sight alone that a conspecific, instead of a non-conspecific, female is present is widespread in the family Salticidae and that it may be routine for salticid males to use information about the presence of conspecific females when making strategic decisions related to escalation during encounters with other males.

Appendix Four

Cross-modality effects during male-male interactions of jumping spiders

Warthog at the Sheldrick Wildlife Trust. Nairobi, Kenya

Pages 306-312 of thesis.

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Cross-modality effects during male–male interactions of jumping spiders

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Abstract

An important prediction from game theory is that the value of a resource influences the level to which male–male conflict escalates. Earlier experimental studies have shown that the seven salticid species we study here (*Bavia aericeps*, *Euryattus* sp., *Hypoblemum albovittatum*, *Jacksonoides queenslandicus*, *Marpissa marina*, *Portia africana* and *Simaetha paetula*) determine by sight whether a female is a conspecific or a heterospecific and then escalate the intensity with which they interact (i.e., they adopt behaviour that is likely to put them at greater risk of injury after detecting the presence of a conspecific female). Here the earlier studies are extended by using the

Appendix Five

Male and female mate-choice decisions by *Evarcha culicivora*, an East African jumping spider

Giraffe at the Langata Giraffe Centre. Nairobi, Kenya

Pages 314-321 of thesis.

Male and Female Mate-Choice Decisions by *Evarcha culicivora*, An East African Jumping Spider

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Abstract

There has been a considerable recent interest in the criteria by which animals choose mates and in the extent to which mating systems tend to be based on mutual mate choice. In this study, we consider *Evarcha culicivora*, a salticid spider from East Africa. This species has some unusual characteristics, including active display by females as well as males, males that kill females more frequently than females kill males and wide intrasexual variation in body size. For females, larger males are especially dangerous. Here, we demonstrate, using two experimental designs (live-mate choice and mount choice), that virgin males, virgin females and previously mated males prefer larger opposite-sex individuals as potential mates, but mated females prefer smaller, safer males as potential mates.

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Appendix Six

Complex display behaviour of *Evarcha culicivora*, an East African mosquito-eating jumping spider

Orphaned elephants playing in the mud at the Sheldrick Wildlife Trust. Nairobi, Kenya

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Complex display behaviour of *Evarcha culicivora*, an East African mosquito-eating jumping spider

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Abstract *Evarcha culicivora*, an East African jumping spider (Salticidae), is an unusual predator because it feeds indirectly on vertebrate blood by choosing blood-carrying mosquitoes as preferred prey. It also associates with particular plant species, *Lantana camara* and *Ricinus communis*. Here we document this species' exceptionally complex display repertoire. In common with many other salticids, *E. culicivora* exhibits pronounced courtship versatility, with males using different tactics depending on the female's location and state of maturity. However, in contrast to most other salticids that have been studied, the males and the females of *E. culicivora* are both active at initiating and sustaining courtship, and both sexes are cannibalistic. Contrary to the emphasis in the literature on female spiders eating males, females of *E. culicivora* run a higher risk of being killed by males than vice versa during courtship. *E. culicivora* males also differ from other salticids that have been studied by adopting pronounced copulatory courtship. Male-female interactions of *E. culicivora* are especially complex when encounters are in the foliage of *L. camara* and *R. communis*.

Keywords copulatory courtship; courtship; Salticidae; sexual cannibalism; spiders

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INTRODUCTION

Most spiders have eyes that lack the structural complexity required for acute vision (Homann 1971; Land 1985), but salticids have a pair of distinctively large forward-facing anterior-medial eyes that support exceptional spatial acuity (Land 1969a,b; Williams & McIntyre 1980; Blest et al. 1990; Harland & Jackson 2004). Not surprisingly, the most elaborate vision-based display behaviour known for spiders (Foelix 1996), and among the most elaborate ever described for any animal group, is found in this family (Crane 1949; Jackson 1982a; Jackson & Pollard 1997; Maddison & Hedin 2003).

Here we provide the first detailed account of how conspecific individuals of *Evarcha culicivora* Wesolowska & Jackson interact during courtship (male-female interactions) and during same-sex interactions. This East African jumping spider (Araneae, Salticidae) is an unusual predator because it feeds indirectly on vertebrate blood by choosing blood-carrying mosquitoes as preferred prey (Jackson et al. 2005; Nelson et al. 2005; Nelson & Jackson 2006) and it is also an unusual spider because it associates with, and feeds on the nectar of, *Lantana camara* L. and *Ricinus communis* L., plant species that grow wild in the same habitat. *Ricinus communis* (family Euphorbiaceae), is native to tropical Africa (Cronk & Fuller 1995), but *Lantana camara* (family Verbenaceae) is native to tropical and subtropical America and has been introduced to many parts of the world as an ornamental plant (Ghisalberti 2000), including East Africa.

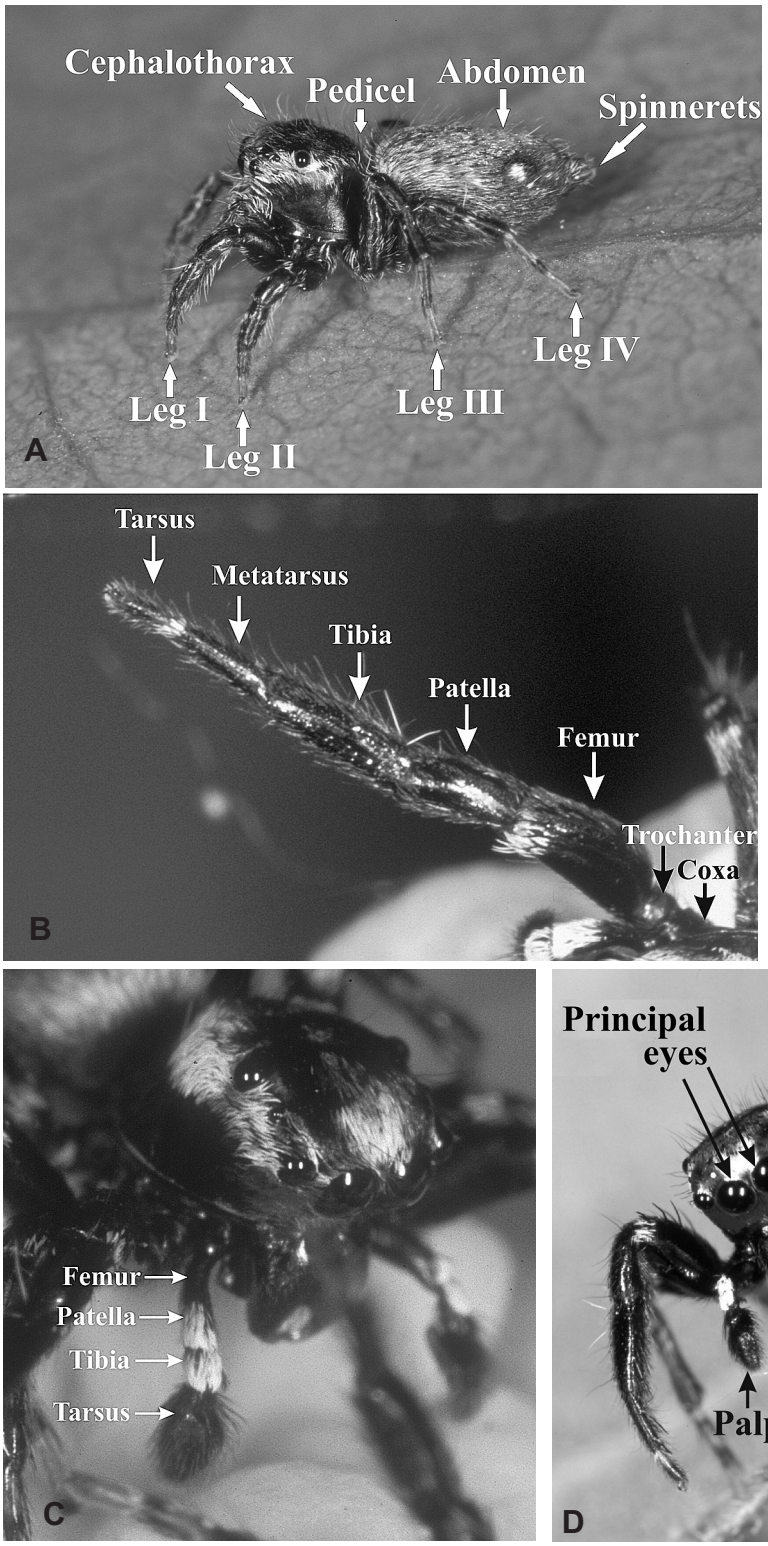


Fig. 1 Male and female of *Evarcha culicivora*, showing anatomical detail important for describing behaviour. **A**, Adult female (facing left) in normal posture showing location of body parts and appendages. **B**, Leg, showing segments. **C**, Palp, showing segments. Note: leg and palp segmentation similar, except for palps having no metatarsi. **D**, Adult male (facing forward) showing eyes, palps, chelicerae and fangs (partially extended). Clypeus ("face") blood red. White patches on carapace immediately behind principal eyes and palp tibia.

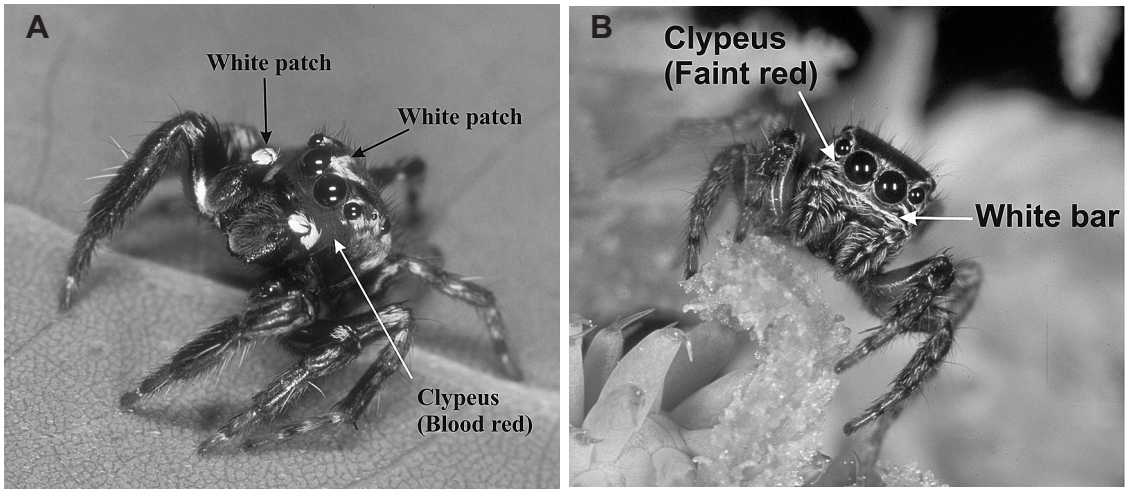


Fig. 2 *Evarcha culicivora* with palps in frontal posture. **A**, Male (facing 45° to left). Face blood-red. White patches above principal eyes, at side of clypeus and on palp tibia. Note: apparent white patch on the leg is an artefact in this photograph from reflected light. **B**, Female on *Ricinus communis* (facing forward). Face with faint red tinge. White bar at bottom of clypeus.

Our objective is primarily qualitative baseline information as a foundation for ongoing work on how *E. culicivora*'s unusual diet and its unusual affinity for particular plant species interrelate with mate-choice behaviour, display function, tactical design and selective attention. We also consider how *E. culicivora*'s intraspecific interactions relate to our understanding of salticid display behaviour in general.

MATERIALS AND METHODS

Our field site was at the Thomas Odhiambo Campus (TOC) of the International Centre of Insect Physiology and Ecology (ICIPE) (Mbita Point, western Kenya). Mbita Point is 1200 m above sea level (0°25′S–0°30′S by 34°10′E–35°15′E) and has a mean annual temperature of 27°C. Laboratory work was carried out at the TOC and at the University of Canterbury (UoC) using cultures established from individuals collected at Mbita Point (for standard salticid-laboratory procedures, see Jackson & Hallas 1986) (for anatomical details that are important for describing behaviour, see Fig. 1 and 2). *E. culicivora*'s laboratory-rearing environment was enriched (see Carducci & Jakob 2000), as we used spacious cages (90 × 90 × 125 mm) with a mesh work of twigs (not from *Lantana* or *Ricinus*) within each cage. A water-logged cotton roll was always present in each spider's cage, and all spiders were fed to satiation on "lake flies" (non-biting midges from the families Chaoboridae and Chironomidae) and on blood-fed female mosquitoes (*Anopheles gambiae ss*) three times a week (Jackson et al. 2005).

Adult males (Fig. 1D and 2A), adult females (Fig. 1A and 2B), and all juvenile stages of *Evarcha culicivora* have grey-brown bodies (Wesolowska & Jackson 2003), but adult males are distinctive because of their blood-red faces and white-hair patches on and around their faces (Fig. 1D and 2A). These white patches are usually, but not always (see Fig. 3) absent from adult females and juveniles. Juveniles have grey-brown faces. The faces of adult females are also grey-brown, but with a faint red tinge. Body lengths of adults are variable (males, 3–6 mm; females, 4–7 mm; see Cross et al. 2007).

Except where stated otherwise, our summaries are for interactions between individuals that were similar in size (i.e., body lengths matched to the nearest mm). Hereafter, unless otherwise specified, the shorter expressions "male" and "female" will be used for "adult male" and "adult female". Earlier convention (Jackson & Hallas 1986) is adopted for indicating frequencies of occurrence: "usually", "often", "typically" and "typical" indicate c. 80% or more; "sometimes" and "occasionally" indicate 20–80%; "infrequently", "rarely" and "on rare occasions" indicate 20% or less.

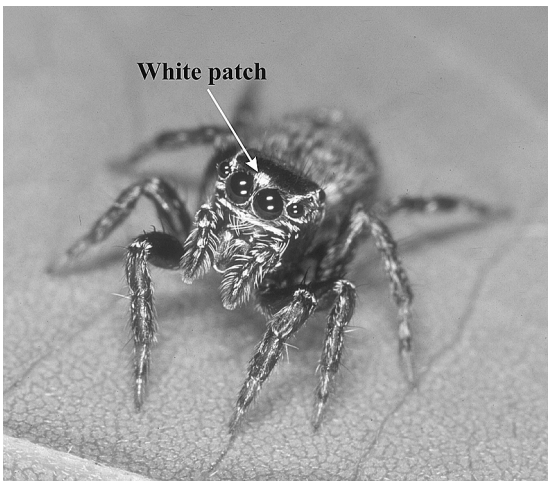


Fig. 3 *Evarcha culicivora* female (facing forward and slightly up and to left) with palps in normal posture. Small white patch above principal eyes.

A "bout" is a period of continuous performance of a particular behaviour pattern (e.g., a bout of palp waving is a period of continuous up-and-down motion of a palp, which may include numerous complete cycles from the most dorsal to the most ventral position and back). "Amplitude" is the distance between the extreme positions in a movement sequence (e.g., for palp waving, the distance between the most dorsal and the most ventral position). The first major segment distal to the joint being articulated is referred to when specifying the site of an appendage's movement (e.g., femoral movement: coxa-trochanter joint).

The following example illustrates how the terms "matching phase", "alternating phase" and "irregular phase" are used. When two palps are waving dorsoventrally at the same time, they are referred to as being in "matching phase" if both are in their most dorsal positions simultaneously. If one palp is in the most dorsal position when the other is in the most ventral position (phase difference 180°), they are "alternating". Irregular phasing is anything between matching and alternating.

Encounters between spiders were staged by putting one spider in the presence of another. We staged male-female encounters, as well as encounters of males with subadult females (subadult: juvenile one moult away from maturity). Male-female encounters were staged with and without a nest present (with the male or with the female the resident of the nest). We also staged female-female and male-male interactions, each with and each without a nest present. However, as males were reluctant to stay inside nests, it was particularly hard to observe interactions in which males were the nest residents.

By definition, an encounter began when one spider fixated the gaze of its principal-eye corneas on the other spider, or on the other spider's nest, and then either maintained fixation for at least 30 s or else began displaying. One spider walking on to the nest of another spider was another criterion for the beginning of an encounter. When an encounter failed to ensue within 30 min, the test was terminated. By definition, interactions began when the spiders began to adopt display behaviour (see below), whereas interactions ended when one spider fled and the other spider failed to watch or follow it for the next 60 s.

Besides staging encounters inside bare cages ("no-plant tests"), as in earlier salticid studies (Jackson & Pollard 1997), we also staged male-male, female-female and male-female interactions (all in the absence of nests) on *L. camara* and *R. communis* ("plant tests"). Plant tests were staged in two ways: (1) leaves and flowers of *L. camara* were placed inside a cage; (2) the spiders were put together on potted *L. camara* or *R. communis* plants sitting on a laboratory bench in the open. All sex-age classes readily walked on to the cuttings and on to the potted plants, and *E. culicivora* was especially inclined to settle on the flowers of *L. camara*, seeming reluctant to leave even when prodded aggressively with a small paint brush.

For staging an interaction inside a cage, with or without a plant present, one spider (the "intruder") was introduced through a hole (diameter 10 mm; plugged with rubber stopper) into a cage already occupied by another spider (the "resident"). For staging an interaction on a plant in the open, first the resident was put on the plant and then, 60 min later, the intruder was put on the plant 15–20 mm away from the resident.

Individuals were chosen at random from the laboratory stock, but no individual was used more than once in any one type of interaction (Table 1). Whether an individual spider was the intruder or the resident was decided at random.

Two broad groupings of behaviour are considered: (1) behaviour that was prevalent during encounters between individuals of *E. culicivora* but also prevalent in other circumstances ("general behaviour"); (2) behaviour that was seen largely, if not exclusively, during encounters between individuals of *E. culicivora*. Besides mating behaviour, the second grouping includes behaviour with an apparent

Table 1 Number of each type of interaction observed for *Evarcha culicivora* during same-size tests (i.e., to nearest millimetre, two individuals matched in body length) and different-size tests (i.e., one individual, in body length, at least 2 mm larger than other individual).

Same-size tests			Different-size tests		
	No. of encounters	No. of interactions		No. of encounters	No. of interactions
Male-female in bare cage; no nest present; resident is female	778	764 (98%)	Male-female in bare cage; no nest present; resident is female; resident is larger	280	277 (99%)
			Male-female in bare cage; no nest present; resident is female; resident is smaller	259	245 (95%)
Male-female in bare cage; no nest present; resident is male	517	485 (94%)			
Male-female in bare cage; nest present; resident is female	781	739 (95%)	Male-female in bare cage; nest present; resident is female; resident is larger	180	160 (89%)
			Male-female in bare cage; nest present; resident is female; resident is smaller	149	136 (91%)
Male-female in bare cage; nest present; resident is male	367	342 (93%)			
Male-female in cage with *Lantana camara*; resident is female	263	248 (94%)	Male-female in cage with *L. camara*; resident is female; resident is larger	138	131 (95%)
			Male-female in cage with *L. camara*; resident is female; resident is smaller	160	154 (96%)
Male-female in cage with *L. camara*; resident is male	283	256 (90%)			
Male-female on potted *L. camara*; resident is female	263	251 (95%)	Male-female on potted *L. camara*; resident is female; resident is larger	161	147 (91%)
Male-female on potted *R. communis*; resident is female	230	206 (89.6%)	Male-female on potted *Ricinus communis*; resident is female; resident is smaller	170	156 (92%)
Male-female on potted *L. camara*; resident is male	270	250 (93%)			
Male-male in bare cage; no nest present	728	713 (98%)	Male-male in bare cage; no nest present; resident is larger	280	272 (97%)
			Male-male in bare cage; no nest present; resident is smaller	265	251 (95%)
Male-male in bare cage; nest present	235	222 (94%)			
Male-male in cage with *L. camara*	327	315 (96%)			
Male-male on potted *L. camara*	263	250 (95%)			
Male-male on potted *R. communis*	220	191 (86.8%)			
Female-female in bare cage; no nest present	354	335 (95%)	Female-female in bare cage; no nest present; resident is larger	189	170 (90%)
			Female-female in bare cage; no nest present; resident is smaller	165	158 (96%)
Female-female in bare cage; nest present	291	255 (88%)			
Female-female in cage with *L. camara*	236	215 (91%)			
Female-female on potted *L. camara*	250	234 (94%)			
Female-female on potted *R. communis*	199	171 (85.9%)			

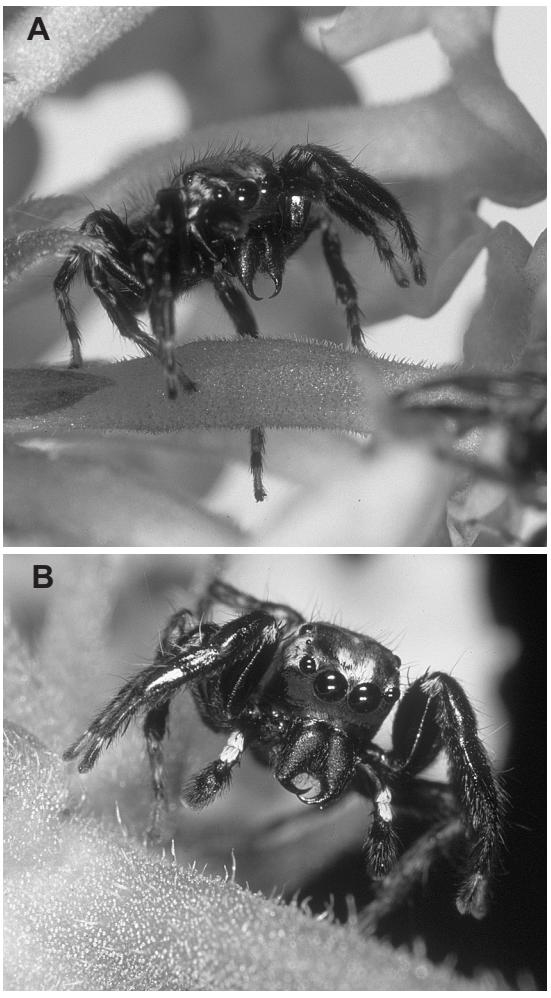


Fig. 4 *Evarcha culicivora* male on *Lantana camara* (facing slightly to right). Posturing with legs arched and chelicerae opened. **A**, Fangs fully extended (i.e., pointing perpendicular down to substrate). Palps in high retracted posture. **B**, Fangs partially extended (held about parallel with substrate). Palps lowered.

communication function ("displays"). Behaviour categories are indicated below in bold, with key variations indicated in italics.

Data were analysed using chi-square tests for goodness of fit (null hypothesis: probability of making one of the two choices same as probability of making the other choice), chi-square tests of independence and Mann-Whitney U-tests (see Howell 2002).

Fig. 5 *Evarcha culicivora* male (facing right) mounted (standing over female) and leaning across right side of the female's flexed-up and rotated abdomen. Female facing left with her cephalothorax lowered (almost touching substrate). Male stroking with his right leg I.

GENERAL BEHAVIOUR

Quiescent individuals of *E. culicivora* typically rested on or close to the ground, usually hidden by tall grass or other vegetation and usually near tree trunks or the walls of buildings. They were also found in concealed places around the inside walls of houses (e.g., behind furniture or in spaces around window panes). Active individuals frequented open spaces on tree trunks as well as on the inside and outside walls of buildings.

In the normal body posture, the spider's body was parallel to, and only 0.5–1 mm above, the substrate. Legs were loosely flexed at various joints, and the abdomen was usually aligned with the cephalothorax (Fig. 1A).

In the normal palp posture (Fig. 3), the palps hung loosely down in front of the spider's chelicerae, with femur-patella joints flexed so that the tarsi were about parallel to each other and perpendicular to the substrate.

During normal locomotion, *E. culicivora* walked in a rapid stop-and-go fashion (e.g., stepping for 0.5 s, pausing for 0.5 s, etc), as is typical of most salticids. If severely provoked (e.g., by a researcher attempting to catch it), *E. culicivora* usually moved away rapidly, sometimes making repeated leaps combined with running. However, compared with most salticids, *E. culicivora*'s normal disposition seemed unusually calm (e.g., compared with many other salticids, *E. culicivora* was less easily provoked

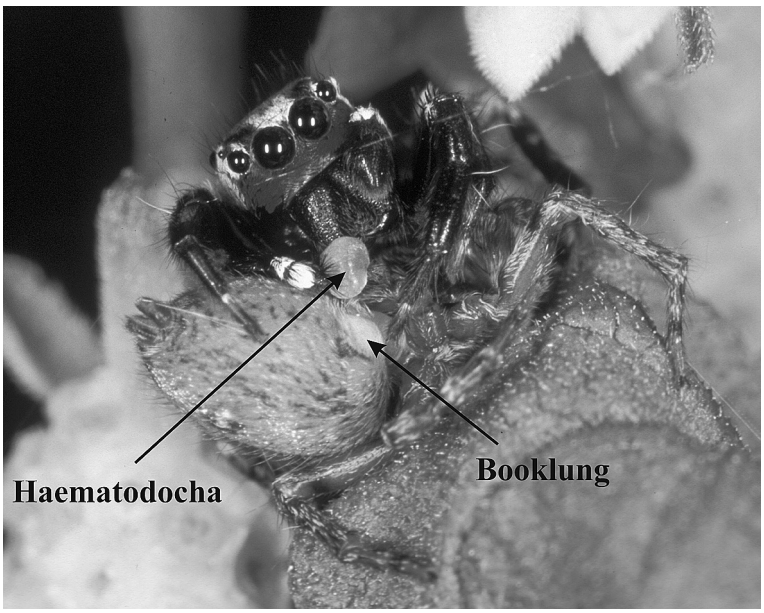


Fig. 6 Male-female pair of *Evarcha culicivora* copulating. Male facing forward, leaning over female's carapace, with tarsi of legs I on ventral surface of female's rotated abdomen. Female's abdomen flexed up and rotated, with cephalothorax lowered (touching substrate). Male's palp applied to female's epigynum (plate on female's anterior ventral abdomen with three pores, one for oviposition and two for receiving sperm from male's two palpal organs), with haematodocha (membranous portion of palpal organ that inflates during sperm transfer) fully inflated and obscuring view of epigynum in this photograph.

into fleeing when being moved about in the course of laboratory observations).

A distinctive predatory posture (legs pulled in close to the body and body being lowered close to, if not touching, the substrate) normally preceded leaping on prey, and often preceded leaping on a conspecific individual.

A spider postured with opened chelicerae (Fig. 4) by holding the basal segments of the chelicerae spread apart (two chelicerae making angle of 45–90° to each other), typically with fangs extended. The degree of fang extension was highly variable. Fully extended: fangs pointing almost straight down (Fig. 4A). Partially extended: any extension of fangs short of fully extended (Fig. 1D and 4B).

Fig. 7 *Evarcha culicivora* male swaying. Legs I and II 90° to body, with tarsi off substrate, palps lowered and abdomen flexed down. Leaning to his right. Viewed from above and side (spider facing left).

POSITIONING OF CEPHALOTHORAX, ABDOMEN AND BODY

When a spider's cephalothorax was raised (Fig. 4B), it was held higher than normal above the substrate, with its anterior end sometimes tilting up 10–45°. When the spider's cephalothorax was lowered, its ventral surface was positioned no more than 1 mm above (Fig. 5), if not touching (Fig. 6), the substrate.

When the spider's abdomen was flexed down (Fig. 7), the spinnerets nearly or actually contacted the substrate, with the angle between the abdomen and substrate being 45–90° (i.e., the abdomen was flexed ventrally from the cephalothorax; cephalothorax always raised). When flexed up (Fig. 5), the spider's abdomen angled up 10–80° from the cephalothorax, the cephalothorax usually being lowered.

Raised body (Fig. 8 and 9B) and lowered body (Fig. 9) refer to instances in which the spider's abdomen was aligned with its cephalothorax (i.e., the abdomen was neither flexed down nor flexed up)

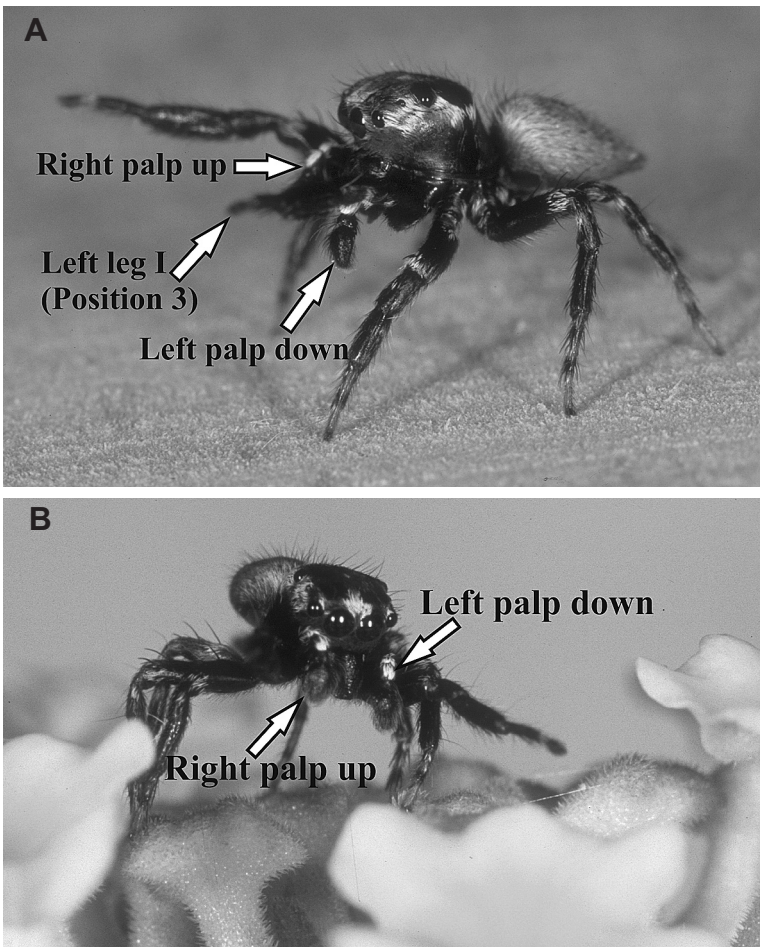


Fig. 8 *Evarcha culicivora* male with raised body. Legs in erect position 3 and palp stepping. **A**, Side view (facing left). **B**, Front view. Male on *Lantana camara* flowers.

and the abdomen and the cephalothorax both were raised or both lowered, respectively.

When flexed to the side, a spider's abdomen was angled 20–45° to either side of the cephalothorax, typically with its body lowered or with its cephalothorax raised and abdomen flexed down.

When a spider had its body tilted up, its cephalothorax and abdomen were aligned (cephalothorax higher and abdomen lower; body-to-substrate angle c. 45°) and the tip of the abdomen was close to, or touching, the substrate.

When a spider had its body rotated to the side (Fig. 10), its legs on one side of the body extended so that its body on that side was elevated. The legs on the other side of the body were pulled in so that this side of the body was held lower than the other side.

When head-standing, a spider angled its cephalothorax down in front by c. 45°, with its abdomen often flexed up c. 45° from the cephalothorax (i.e., the abdomen angled up c. 90° to the substrate). Legs II–IV (sometimes legs I–IV) were held out to the side and flexed down c. 90° at the femur-patella joints, with tarsi on the substrate, legs I and II often being especially close together. Legs I were sometimes in erect position 3 (see below). Head-standing bouts lasted 1–30 s.

Twitch abdomen: a spider moved its abdomen rapidly up and down from the pedicel (amplitude 0.5–1 mm; rate 10–20/s; bouts highly variable in duration, lasting from less than a second to many minutes).

POSTURES AND MOVEMENT OF LEGS

Raised legs (refers to legs I only) were either erect (all joints distal to the femur-patella, and some-

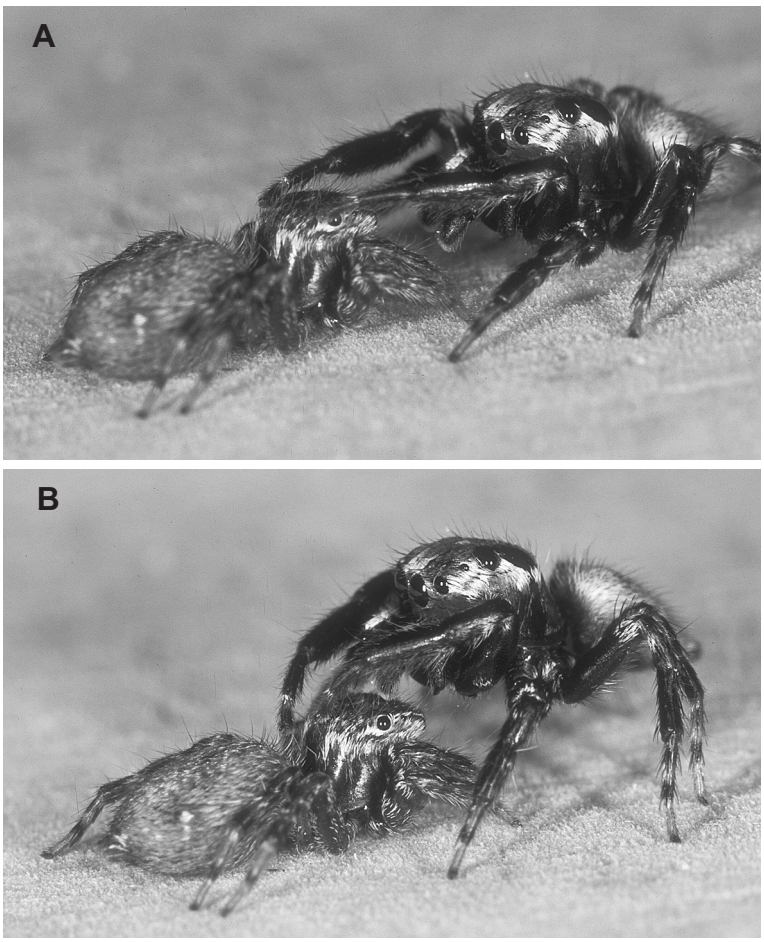


Fig. 9 *Evarcha culicivora* male (on right, facing left) tapping (using legs I) female (on left, facing right). Female's body lowered. **A**, Male erect taps (position 2) (palps semi-erect in position 1). **B**, Male flexed taps (legs no longer erect) while raising body and beginning to mount female.

times the femur-patella joints as well, were fully extended) or semi-erect (not quite fully extended). Sometimes there was superimposed bowing (Fig. 11, 19) of erect legs (i.e., there was slight angling down at the femur-patella joint and slight angling up at the tibia-metatarsus joint, and sometimes at the metatarsus-tarsus joint as well). Six modal positions were discernible.

In position 1 (Fig. 11), the two legs were held parallel to each other and, at least from the patellae to the tips of the tarsi, parallel to the substrate (i.e., tarsi pointed straight forward, but sometimes the femora were angled up with comparable downward flexion of the femur-patella joint so that, from the patella forward, the leg was parallel to the substrate). There were two modal versions of position 1. In extended position 1, the spider's femur varied from straight forward (Fig. 11) to up by as much as 45°. In flexed position 1, the spider's femur was angled straight

Fig. 10 *Evarcha culicivora* male rocking to side (in this frame, body rotated down on his left). Legs erect in position 3. Palps lowered.

Fig. 11 *Evarcha culicivora* male (on right) with legs I erect in extended position 1. Male's legs I bowed. Female (out of focus) immediately in front of and facing male.

Fig. 12 *Evarcha culicivora* female (on right) with legs I erect in flexed position 1. Male flexed taps female's carapace with his right leg I. Female's abdomen rotated (dorsal surface in view in photograph) and slightly raised.

up, or almost straight up, with the femur-patella joint flexed 90° (Fig. 12).

Position 2 (Fig. 13) was similar to position 1 (extended or flexed) except that, instead of being parallel, the two legs were angled toward each other so that the two tarsi almost or actually touched, or else crossed over by as much as 2 mm.

In position 3 (Fig. 8; spider below in Fig. 15A), the femur extended 20–45° out to the side and up by 45–90°, with the femur-patella joint flexed down so that the tarsus pointed anywhere from down by 45° to up by 45°.

In position 4 (Fig. 14), each leg was held straight or almost straight (i.e., there was little or no flexion at the femur-patella joints) and the tarsi were angled out to the side by 20–45° and up by 20–45°.

In position 5 (spider above in Fig. 15), the leg was pulled back 90° to the sagittal plane of the spider's body. The femur extended up by 45–90° and the femur-patella joint flexed down so that the tarsus was pointing anywhere from down by 45° to up by 45°.

Position 6 (spider below in Fig. 15B) was similar to position 5 except that the femur-patella joint was not flexed down, or else it was flexed down only slightly, so that the tarsus pointed 75–90° up.

Before flicking, legs I were arched (see below) or, more often, in erect position 3. A spider flicked by suddenly and rapidly moving one leg I (Fig. 16) or both legs I up c. 1 mm (upward motion taking 0.1 s or less) and then, after a momentary pause, moving the leg or legs less rapidly back down (downward motion taking c. 0.25 s). When both legs flicked, they moved in matching phase.

When striking, one spider brought its erect legs I (positions 3 or 4) rapidly and forcefully down and forward. At the end of the strike, legs I extended forward in position 1 or 2, but now semi-erect instead of erect, and tarsi contacted the other spider or the substrate just in front of the other spider.

Fig. 13 *Evarcha culicivora* male (facing down in photograph) on *Ricinus communis* leaf with legs I erect in position 2, extended over female's carapace. Female facing up in photograph, with body lowered.

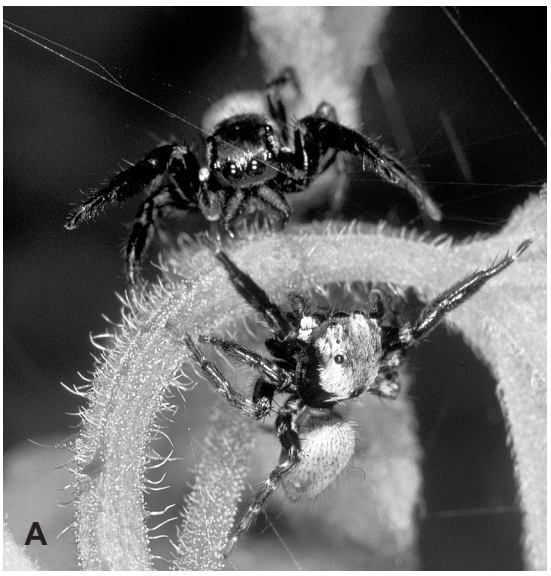
Arched legs (Fig. 4): legs I, or legs I and II, held about 45–90° to the side of the body (femur angled up 45–90°; femur-patella joint flexed so that patella and tibia angled down 20–45°; slight flexion (10–20° usual) at the tibia-metatarsus joint; tarsi on or close to the substrate).

When hunched (Fig. 17), legs I–III were held to the side of the cephalothorax (i.e., pulled back so that they were largely behind the chelicerae) and were highly flexed, especially at the femur-patella joints. Leg tarsi, especially tarsi I, were often held above, but close to, the substrate. When loose hunching (Fig. 17A), tarsi angled about perpendicular to the substrate, whereas they angled inward by as much as 45° when tight hunching (Fig. 17B). While hunching, the spider sometimes held its cephalothorax raised, its abdomen flexed down and its palps in the low-retracted posture (see below).

From the hunched posture, especially when with cephalothorax raised, a spider wagged by rapidly raising legs I (taking c. 0.2 s) and then more slowly returning the legs to the tight hunched posture (taking c. 0.5 s). Leg raising was primarily by extension of the femur-patella joints. When maximally raised during a wagging cycle, legs were usually erect or semi-erect (position 5 or 6). Usually both legs moved at the same time, and usually phasing was matching, although there were rare instances of phasing being irregular and of only one leg I wagging.

Males froze by remaining immobile, all the while holding legs hunched or erect.

Fig. 14 *Evarcha culicivora* male (on right) on *Lantana camara* flowers with legs I erect in extended position 4. Female departing by walking away (cephalothorax between two flowers; only abdomen visible in photograph).



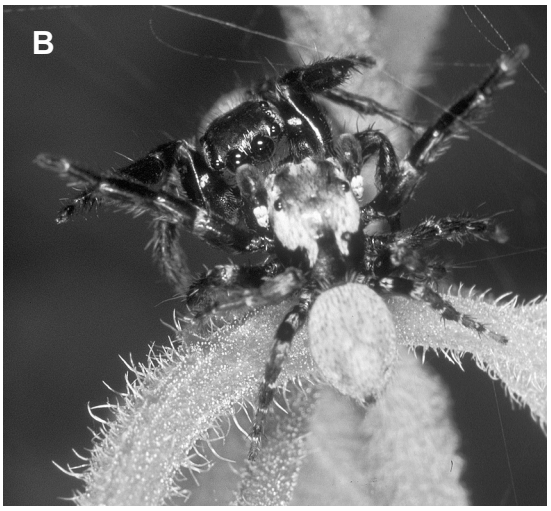


Fig. 15 Two *Evarcha culicivora* males on *Ricinus communis*. **A**, Male at top of photograph (front-on view) with legs erect in position 5 (tarsi angled down 45°) and palps in high retracted posture. Chelicerae opened, with fangs fully extended. Male below (dorsal view), with left leg I erect in position 3 and right leg I on leaf, moving toward male at top. **B**, Initiation of an embrace. Male at top has legs erect in position 5 with femora 90° up and rest of leg parallel to horizontal plane. Male below has legs I erect in position 6.

Before embracing, two spiders approached each other (Fig. 15A), both with legs hunched, both with legs erect (position 3 or 4) or one with legs hunched and the other with legs erect. Once within c. 5 mm of each other, the spiders moved their legs into erect position 5, continued to advance and sometimes

Fig. 16 *Evarcha culicivora* female on *Ricinus communis* (facing forward) flicking her left leg I (position 3). Palps in high retracted posture.

moved legs to erect position 6, and then brought their faces, legs I and chelicerae into contact (Fig. 15B). Chelicerae were usually open, with fangs extended. While continuing to stand face-to-face, with cephalothoraxes raised and legs I held out to the side and touching, the embracing spiders often moved their legs up and down by as much as 45°, sometimes with tarsi moving down to where they touched the substrate.

POSTURES AND MOVEMENT OF PALPS

Frontal palps (Fig. 2) were held in front of the face; femora extending almost vertically upward, with the rest of each palp angling straight down and almost pressed against the palp femur. The tips of palp tarsi were about even with the bottom of the chelicerae. The distance between the two palps in front of the spider's face varied from almost touching to 2 mm apart.

Retracted palps were similar to frontal palps except that, when retracted, the two palps were pulled back to the side of the spider's face instead of being held in front of the face. In the low retracted position, the palps' tarsi tips were even with the bottom of the chelicerae (Fig. 18). In the high retracted position (Fig. 4A, 16), palps were raised higher (tarsus tips above the bottom of the chelicerae). Held in the high-retracted position, the palps were only faintly visible when the spider was viewed front on.

Lowered palps (Fig. 4B, 7, 10) were held to the side of the chelicerae, with sharp flexion at femur-patella joints so that from the patella each palp angled

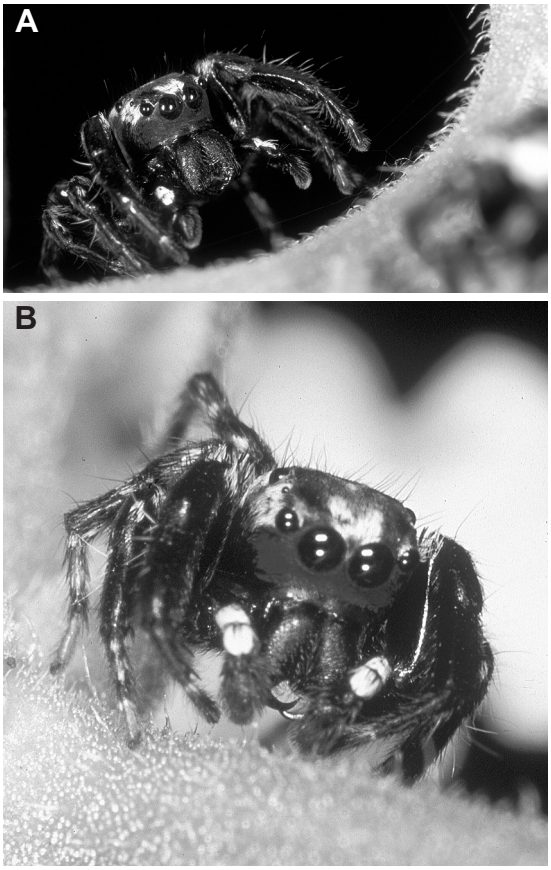


Fig. 17 *Evarcha culicivora* male on *Ricinus communis* with legs in hunched posture. **A**, Loose hunching. **B**, Tight hunching.

Fig. 18 *Evarcha culicivora* male (facing forward) with palps in low retracted posture.

Fig. 19 *Evarcha culicivora* male (head-on view) with legs erect in position 3 and bowed. Palps kinked.

down (sometimes slightly rearward, forward or inward). Femora were about parallel to the substrate and tarsi were considerably below the chelicerae.

Raised palps were either erect or semi-erect. Forward position 1: two palps extended forward about parallel to each other and to the substrate, with all joints fully or almost fully extended (i.e., like legs in erect and semi-erect position 1). Forward position 2: palps held extended forward, about parallel with each other or diverging by as much as 20° or converging by as much as 20°; femora angled up c. 20° and rest of each palp angled down c. 20° because of c. 20° flexion at femur-patella joint. Forward position 3: (i.e., similar to forward position 2 except that each femora angled up c. 45° and the rest of each palp angled down c. 45–90°).

Kinked palps (Fig. 19) were held with each femur angled up 45–90°. Each palp's patella and tibia were held about parallel with the substrate, or angled down by as much as 20°, and also angled in by 20–45° so that they were converging toward each other. Tarsi angled down and back by 20–45° and outward by as much as 20° so that they diverged slightly from each other.

Fig. 20 *Evarcha culicivora* male with legs arched, chelicerae partially opened and palps arched in position 1.

Femora of arched palps extended ventro-laterally alongside, or angled slightly forward from, the chelicerae. The rest of the palp angled ventro-medially so that the tips of the palps converged toward each other. When palps were in position 1 (Fig. 20), tarsi were not under the chelicerae, but tarsi were held under the chelicerae in position 2.

From the normal palp posture, there were two common and distinctive ways in which *E. culicivora* moved its palps. Palp waving was adopted by males, females and juveniles of both sexes, but only adult males adopted palp stepping.

Waving palps moved up and down in matching phase (amplitude 1–2 mm; 1–4/s; bout duration 1 s to 10 min or longer, with c. 10 s being typical; movement femoral and tibial: femora moved forward and up, and at the same time the femora-patellae joints were continuously adjusted so that, distal to the femora, the palps stayed oriented straight down). While the palps were being waved, the tips of their tarsi usually moved from below to above the fangs, but there were also occasions when the tips of the spider's palps stayed below or above the fangs.

When palp stepping (Fig. 8), femora moved up and forward, with the rest of each palp remaining straight (i.e., flexion of the femur-patella joint changed, but there was little or no change in the flexion of the other palp joints). The two palps moved up and down in alternating phase (amplitude 0.5–3 mm, 1–5/s), the result being that the two palps moved as though walking in the air. The tips of the tarsi usually went from below to above the fangs in each cycle, but there were also periods when they remained above or below the fangs. Simultaneous with the palps moving up and down, a slight side-to-side wobble of the palps was often noticeable.

With palps lowered, a spider performed side-to-side palp waving by repeatedly moving its two palps inward and then outward (c. 1/s, 2–3 mm). There were two variations. In-and-out: both palps moved in together and out together. Left-right: the spider moved both of the palps together to the left (or right) and then both palps together to the right (or left).

PROPULSIVE DISPLAYS

A collective term, propulsive displays, is used for charging, long leaping, lunging, ramming, spurting, striking and truncated leaping (i.e., displays that entail sudden and rapid movement toward another spider).

A spider charged at another spider by suddenly running forward 10–40 mm and, when about one body length in front of the other spider, suddenly stopping.

A spider made a long leap by jumping 50–70 mm towards, and sometimes making contact with, another spider. When contact was made, the leaping spider did not hold on.

A spider lunged by moving its body forcefully forward 1–2 mm, achieving this by suddenly and rapidly extending legs III and IV rearward without the tarsi of these legs leaving the substrate.

Ramming was the same as charging except that, instead of stopping, the advancing spider kept going and contacted the other spider, usually head-on.

A spider spurted by stepping toward another spider in a rapid stop-and-go manner. The duration of each burst of moving forward and of each pause was about 0.25 s.

A spider made a truncated leap by suddenly jumping 5–10 mm toward, but not making contact with, another spider.

JERKING BACK, ROCKING, SWAYING AND STEPPING

A spider jerked back (Fig. 21B) by suddenly moving its body forcefully backwards 1–2 mm, achieving this by suddenly and rapidly extending legs II and IV (and sometimes also legs I) forward without the tarsi of these legs leaving the substrate.

A spider rocked forward and backward by repeatedly moving its body first forward and then backward (amplitude 2–4 mm, 2–3 cycles/s, bout duration

Fig. 21 *Evarcha culicivora* male and female, each on a different *Lantana camara* flower. Male (upside down, on left). **A**, Female (on flower on right) walking (abdomen in view). Male, partially hidden under flowers, emerges and postures with legs in erect position 3. **B**, Female (on right) jerks back while facing male (on left).

usually 1–2 s). This was achieved by extending and then flexing its legs III and IV without stepping (i.e., the spider's tarsi remained on the substratum). Typically the spider had legs erect in position 1, 2 or 3 when it rocked forward and backwards. Except for being faster and at considerably smaller amplitude (5–10/s, <1 mm, 5–10 cycles per bout), shaking resembled rocking forward and backward.

When rocking side to side (Fig. 10), a spider rotated its body to the left (or right) and then, usually without pausing, to the right (or left) (amplitude 10–45°, 1–2 cycles/s, one cycle per bout). Legs I were usually in erect position 3 when the spider began to rock, but the leg I on the side of the body being lowered typically went down to the substrate and then was elevated to erect when this side of the body moved upward, with the opposite leg now going down to the substrate.

A spider swayed (Fig. 7) (i.e., moved its cephalothorax from side to side) by flexing the legs on one side and simultaneously extending the legs on the other side. There was no stepping (i.e., the spider's legs remained on the substrate). When the spider combined hunching with swaying, legs I, II and III were more strongly flexed on the side toward which the cephalothorax was moving. The sagittal plane of the cephalothorax remained perpendicular to the direction of movement, but the posterior tip of the spider's abdomen usually stayed in place (i.e., the abdomen-cephalothorax angle usually changed during swaying so that the abdomen was alternately flexed to the right and flexed to the left). Each swaying cycle (left, right, and back, or right, left, and back) took 0.5–1 s (body moved 2–4 mm) and the spider swayed as many as four times in a row before pausing. Simultaneous with swaying, the spider sometimes tilted its body 45° down on the side toward which it moved.

When stepping to the side, a spider walked sideways 5–10 mm in one direction, paused for c. 0.5

s, and then walked sideways 5–10 mm in the other direction. One or both legs I were usually held erect in position 3, and sometimes a spider flicked one or both legs I while stepping. When only one leg was flicked, it was usually the leg on the side toward which the spider stepped. When both legs were flicked, the leg on the side toward which the spider stepped moved up sometimes before the leg on the other side moved up. Sometimes, the spider also changed speed of stepping to faster or slower before changing direction.

Two modes of stepping to the side were discerned: smooth and jerky. Smooth: neither the beginning nor the ending of stepping was abrupt. Jerky: stepping abruptly began and abruptly ended, individual steps were shorter, and the spider's stepping gait had a distinctive up-and-down component.

Only males danced, and they danced only in male-female interactions. When linear dancing, a male stepped forward and then, either immediately or after a brief pause, stepped backward, usually repeating the sequence 5–10 times before taking a longer pause or stopping. While facing a female, a male zigzag danced by stepping to one side, pausing briefly, and then stepping to the other side, usually repeating the sequence 5–10 times before taking a longer pause or stopping.

By stepping slowly forward 1–3 mm, then pausing, then stepping forward 1–3 mm again, and so forth, a spider eased forward (i.e., one spider moved gradually towards the other spider). While easing forward, the spider's body was held lowered, and usually legs I were in erect position 1. Spiders were usually no more than about five body lengths apart when they began easing forward.

When a spider departed (Fig. 14 and 21A), it left the vicinity of another spider by stepping away at more or less normal walking speed.

A spider fled by running, and sometimes by leaping, quickly away.

When one spider fled, the other spider chased it by running, and sometimes by zigzag dancing or leaping, all the while following closely behind the fleeing spider.

Quiescent: male and female stationary, female usually in the normal posture and male usually frozen in erect posture or, in rare instances, frozen in the arched or hunched posture.

Quiet: male and female not very active, more or less stationary, but with the male repositioning his legs intermittently.

NESTS

Evarcha culicivora's nest (Fig. 22) was a silk tube (length and width 4–6 times the body length and width, respectively, of the resident spider) with one or more elastic openings ("doors"). In the field, nests were typically built in the enclosed spaces formed by dead, rolled-up leaves ("detritus"). The detritus used as nest sites was typically mixed in with grass growing near the ground beside tree trunks, the walls of buildings and boulders. It was also common to find nests in the detritus found in spider webs (undetermined species of *Argyrodes* (Theridiidae), *Cyrtophora* (Araneidae), *Nephilengys* (Nephilinidae) and *Tetragnatha* (Tetragnathidae); undetermined genera of Agelenidae, Araneidae, Pholcidae and Theridiidae).

Whether a nest had one or two doors (or, rarely, three doors) appeared to depend on the space available. For example, nests were sometimes wedged in at the narrow end of the cone-like space made by a dead leaf that was tightly rolled-up at one end. In these instances, there was only one door (opening at the wider end). In the laboratory, we sometimes cut pits in the corks used to plug holes in the tops of the cages, with the pit on the side of the cork facing into the cage. *E. culicivora* readily adopted these holes as sites for one-door nests that opened into the cage.

BEHAVIOUR PATTERNS THAT OCCURRED EXCLUSIVELY IN THE PRESENCE OF NESTS

With fangs in the nest silk, a spider chewed by opening and closing the basal segments of its chelicerae (rate, amplitude and bout length highly variable).

Holding down silk was performed by a spider inside a nest. First it moved legs I up and contacted the silk with its tarsi. By lowering its legs, it then pulled the upper silk layer down against the lower layer. How long the spider held the silk down in this fashion varied from a few seconds to several minutes.

When palpating on a nest, a spider's palps moved up and down in a way that resembled how its palps moved when waving, except that tarsi were usually extended more forward. Repeated contact was made with the silk on down strokes.

A spider probed (Fig. 23) by moving legs I forward and backward (1–2 mm, c. 2/s, alternating phase) so that the tarsi jerkily pushed and pulled on the silk.

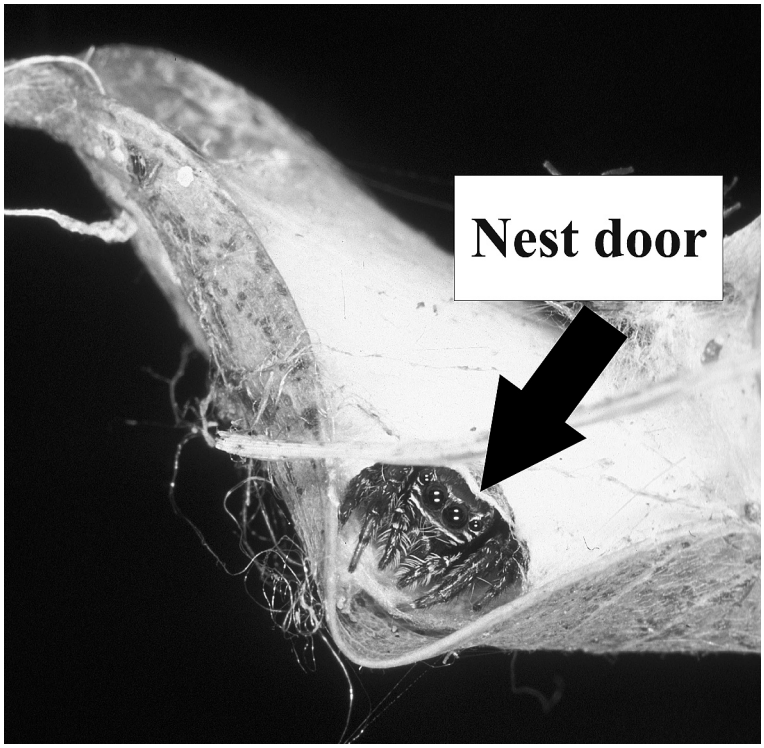


Fig. 22 Nest on dead leaf inside web of *Nephilengys* sp. *Evarcha culicivora* female facing out of nest door. Palps in normal posture.

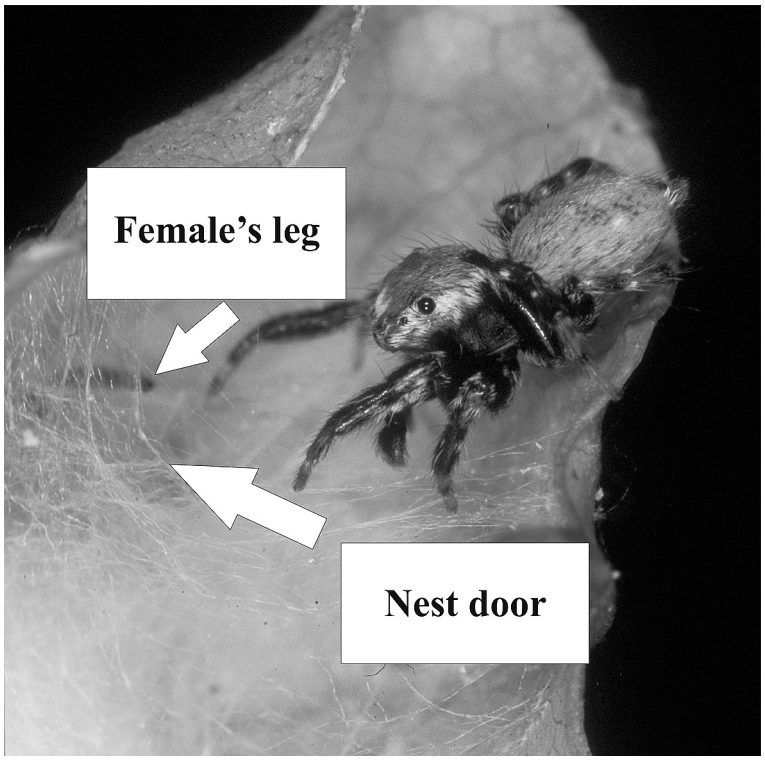


Fig. 23 Nest on dead leaf inside web of *Nephilengys* sp. *Evarcha culicivora* male (facing left) probes at nest door. Female in nest (only her legs I visible in photograph).

Fig. 24 *Evarcha culicivora* male (facing right) erect tapping female (facing left). Male's legs I in erect position 2. Female with legs I erect in position 3.

POST-CONTACT BEHAVIOUR

With his legs in erect position 1 or 2 and held over a female, a male erect tapped with legs (Fig. 24) by moving legs I up and down (movement femoral; c. 2/s; 1–2 mm; alternating, irregular or, most often, matching phase), so that tarsi I repeatedly contacted the female. Erect tapping was concentrated on the female's legs I, carapace and anterior abdomen. Later, as he stepped forward and began to mount, the male switched to flexed tapping, usually with tarsi first hitting the female's carapace, then her anterior abdomen (Fig. 25A) and then more posterior parts of her abdomen as he moved further over the female (Fig. 25B). When flexed tapping, legs moved similarly to how they moved when erect tapping, but there was considerably more flexion at the femur-patella and tibia-metatarsus joints. On rare occasions, males erect tapped briefly with a single leg I, but flexed tapping with a single leg was not seen.

A male quivered by moving erect legs I (position 1 or 2) up and down very rapidly (c. 10/s) and at low amplitude (0.5 mm). Bouts usually lasted 0.5–1 s.

A male palpated on a female in much the same way as he palpated on silk. There were two variations. Standing immediately in front of a female and facing her, a male forward palpated by repeatedly touching a female's face with his palps raised in forward position 1. This was normally a preliminary to mounting. A male flexed palpated (Fig. 26) while standing over a female, his palps flexed considerably and tarsi repeatedly contacting the female's carapace or dorsal abdomen. Once a female rotated her abdomen, males sometimes also flexed palpated on the side or bottom of the female's abdomen.

Males mounted by walking over females, and there were three primary ways in which they did this: (1) the male first walked toward a facing female with legs I erect (position 1 or 2), quivered these legs over the female for variable, sometimes long, periods and then moved continuously over her until mounted; (2) as the male zigzag danced in the female's direction, he continued advancing and moved over her without pausing or after only a momentary pause; (3) the male stepped towards the female with his legs I erect (usually in position 1 or 2) and, when he got his legs I over the female, he moved in short spurts of 0.5–1 mm at a time until he gradually moved completely over her.

Before the male engaged a palp to begin copulation, the female always adopted a posture with her cephalothorax lowered and her abdomen raised and rotated (Fig. 5 and 6). Rotated abdomen: female's abdomen rolled c. 90° to the left or to the right, so that its ventral surface moved closer to the male. Before, after or simultaneous with rotating, females flexed their abdomens up. Females sometimes rotated their abdomens while the male was erect or flexed tapping but before he began to mount (Fig. 12).

Once mounted, the male leaned to his left or his right. However, before or while leaning to his left or right, and before or after the female rotated her abdomen, the male sometimes rubbed (Fig. 26) by moving the tips of his tarsi I across the female's abdomen (movement femoral; <1 mm; bout length c. 1 s; tarsi stayed in contact with the female) by repeatedly flexing and extending the tibia-metatarsus joint. The male rubbed with one or both legs, and phasing was highly variable. Depending on how far the female's abdomen had rotated, tarsi were in contact with the dorsal, lateral or ventral surface of the female's abdomen.

As the male leaned further to his left (or right), he brought his right (or left) leg I over and stroked by moving the side of this leg's tarsus (and sometimes also metatarsus) repeatedly across a female's ventral abdomen (1–2/s, 1–2 mm, bout length c. 1 s, tarsus stayed in contact with the female).

There were two categories of scraping, with legs and with a palp, both being performed only by males and only when females had their abdomens rotated but before palp engagement (i.e., not while mating). When scraping with legs (Fig. 27), both legs I moved up and down on the female's ventral abdomen (2–3 mm; c. 2/s; matching phase; tarsi remaining in contact with the female's abdomen for all or most of

Fig. 25 *Evarcha culicivora* male (facing left) flexed tapping female (facing right) as he mounts. Female with body lowered. **A**, Male's tarsi I contacting anterior dorsal abdomen of female just behind pedicel. **B**, Male's tarsi contacting posterior dorsal abdomen of female.

Fig. 26 *Evarcha culicivora* male (facing right) standing over female (below, facing left). Female's abdomen raised and beginning to rotate. Male flexed palpates and also rubs right side of female's abdomen with his left leg I.

Fig. 27 *Evarcha culicivora* male (head on in photograph) scraping posterior ventral abdomen of female with both legs I and with his left palp. Female's abdomen raised and rotated (female's spinnerets forward in photograph).

the time; contact usually posterior to, but close to, the female's epigynum). When scraping with a palp, the male moved the palp that was closer to the female back and forth (2–4/s, c. 0.5 mm) across the ventral surface of her abdomen (Fig. 27), usually on or close to her epigynum (tarsi remained in contact with the female's abdomen for all or most of the time). Bout length for palp scraping was usually c. 2 s, although longer bouts (up to 2 min) were also seen.

Kicking (Fig. 28) was a distinctive manner in which males moved legs IV during mating. Simultaneous kicking with both legs IV was usual, but males kicked on rare occasions with only one leg IV, holding the other leg IV quiescent on the substrate or in the air. Kicking legs moved up and down in matching phase. Before kicking, the male held legs IV elevated (Fig. 28A) so that tarsi were in the air and there was conspicuous flexion at the femur-patella (c. 90°) and tibia-metatarsus (c. 45°) joints. Just before kicking began, legs IV often were slowly elevated higher. Then the spider kicked by suddenly and forcefully moving the whole of each leg down

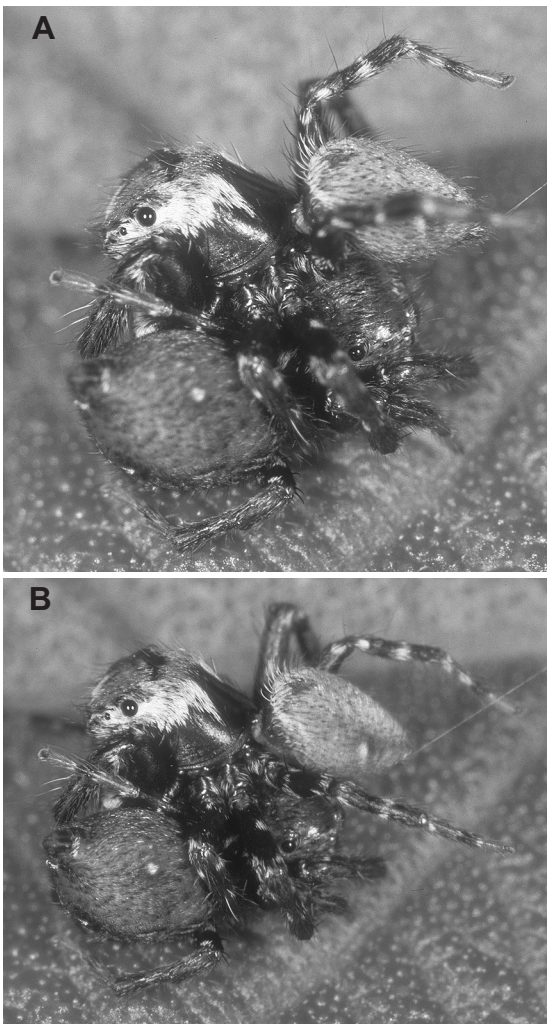


Fig. 28 *Evarcha culicivora* male kicking with legs IV while mating. Male above, facing to left. Female below, facing to right. Male leaning to his right. Female's abdomen raised and rotated. **A**, Male's legs IV elevated preceding kick. **B**, Male's legs IV moving down during kick.

(Fig. 28B). Sometimes, as the two legs moved down, they simultaneously moved slightly toward each other. Sometimes the femur-patella joints also flexed while the legs moved down. Often there was also a superimposed quivering movement of legs IV (up and down, >10/s, <1 mm) during the down stroke. At the end of the down stroke, legs IV stopped while still suspended in the air or else they hit one or more of the female's legs, the substrate or, on rare occasions, the female's cephalothorax.

Intermittent kicking was usual (kicked once and then paused, or kicked 2–6 times in a bout and then paused), but there were rare instances of males kicking continuously for several seconds to many minutes at a time. Amplitude was usually 2–3 mm. Kicking often began fast, and then it slowed down. For example, kicking rate sometimes began at c. 1/s, but soon slowed down to one kick every 2–3 s. As the male kicked, his legs IV went down fast, but then moved up more slowly, with a pause of 0.25–0.5 s between the leg reaching the lower position at the end of the down-stroke and going back up again. Initially the intervals between kicking bouts tended to be 2–3 s, but then they became less predictable and often longer. Males sometimes held legs IV elevated during these intervals.

BEHAVIOUR SEQUENCES

Most behaviour categories were performed by males and by females, in intra- and in inter-sexual interactions (Table 2). However, the manner in which behaviour categories were combined was exceedingly variable, especially in male-female interactions away from nests. The convention we follow here is to use the expression "sequence" for a combination of behaviour patterns, and below we will provide a largely qualitative summary of how sequences varied across the different kinds of interactions we investigated.

How male-female interactions began

The prevalent pattern in salticids is for the male to initiate male-female interactions by displaying first (Jackson & Pollard 1997), and this trend held for *E. culicivora* during male-female interactions when the female was inside, but not when she was outside, her nest. When encounters began outside nests, males sometimes displayed and approached first, with mutual displaying beginning only after the male came to within a few body lengths of the female. However, sometimes females displayed and approached first, with mutual displaying beginning only after the female came to within a few body lengths of the male (i.e., for *E. culicivora*, it was common for either the male or the female to initiate display).

Regardless of whether the male or the female displayed first, initial displays tended to be posturing, with males more often beginning with erect posturing and females more often beginning with hunched posturing. Females sometimes, but males only rarely, initiated interactions by performing propulsive displays (especially charging), and

there were infrequent instances of males initiating male-female interactions by immediately starting to dance.

How waving and stepping with palps were integrated into sequences

In same-sex and male-female interactions, as well as when stalking prey, when walking about and generally when looking at objects of interest, it was routine for females to wave their palps and for males not only to wave their palps but also to step with their palps. Males frequently switched between palp stepping and palp waving, and sometimes there were dozens of switchovers in a row in bouts that lasted several minutes or longer. During these bouts, males sometimes paused briefly before switching, but they more often went from waving to stepping, or vice versa, without pausing.

Table 2 Categories, and dominant variations in categories, of behaviour seen during intraspecific interactions of *Evarcha culicivora* and the types of interactions in which they are used. A, Away from nests; N, on silk at nests; P, postmount; X, not seen.

	Male-female	Female-male	Male-male	Female-female
Arched-legs posturing	A	A	A	A
Chase	A	A	A	A
Chew	N	X	N	N
Dance and spurt forward	A	X	X	X
Ease forward	N	A	X	X
Embrace	A	A	A	A
Erect-legs posturing*	A	A	A	A
Flick legs	A	A	A	A
Freeze	A	X	X	X
Head stand	X	A	X	A
Hold down silk	X	N	X	N
Hunched-legs posturing	A	A	A	A
Kick	P	X	X	X
Mount	P	X	X	X
Open chelicerae	A	A	A	A
Palpate on female	A, N	X	X	X
Palpate on nest	N	X	N	N
Palp waving	A, N	A, N	A, N	A, N
Palp stepping	A, N	X	A, N	X
Probe	N	N	N	N
Propulsive displays†	A	A	A	A
Pull and hold	X	N	X	N
Quiver	A	X	X	X
Rock	A	A	A	X
Rub	P	X	X	X
Scrape	P	X	X	X
Shake	A	A	A	A
Side-to-side palp waving	A	A	A	A
Step to side	A	A	A	A
Strike	A	A	A	A
Stroke	P	X	X	X
Sway	A	A	A	A
Tap	A, N, P	X	X	X
Twitch abdomen	A	A	A	A
Wag	A	A	A	A

*Erect-legs posturing was seen in all types of interaction, except that positions 1 and 2 were only employed in male-female and female-male interactions.
†Propulsive displays were seen in all types of interaction, except females did not ram when interacting with other females.

How dancing and spurting forward were integrated into sequences

Dancing and spurting were behaviour patterns performed only by males and only in male-female interactions. They tended to occur together in complex, variable sequences. Zigzag dancing was especially elaborate and highly variable, the most common pattern being for a male to lower (or raise) his body and step to the side, pause and raise (or lower) his body, and then step to the side again.

When zigzag dancing, movement to the side was typically on an arc, with successive arcs bringing the male closer to the female. While stepping to the side, either the male kept his legs I erect and stepped with legs II–IV or else he lowered his legs I and used them for stepping as well. There were rare occasions when dancing males held their bodies raised while stepping, but dancing males usually held their bodies lowered. Males often tilted their bodies to the side toward which they were moving. Although males sometimes arced back-and-forth 30 or more times before pausing, 3–5 arcs per bout was more typical. When a dancing male paused between steps, he usually had his body raised and his legs I in erect position 1, 2 or 3, and usually he stepped rapidly with his palps (c. 4/s being typical). Males often alternated between erect posturing (in positions 1, 2, 3 and 4) and zigzag dancing, and posturing periods between dancing bouts varied greatly in duration, sometimes lasting for 20 min or longer.

Between bouts and within single bouts, the speed of the zigzag dance was highly variable, with the male on rare occasions slowing down and speeding up even while stepping in one direction on a single arc. There was a tendency for males to step faster when closer to the female and slower when further away. Arc amplitude (i.e., how far the male moved to the left or the right before changing direction or stopping) was typically 20–50 mm, but there were rare occasions when it was as much as 80 mm or more. Dancing tended to be faster when arcs were wider, but there was no clearly discernible relationship between the amplitude of arcs and a male's distance from a female.

Females only sometimes turned their bodies so as to remain oriented toward the zigzag-dancing male. When a male danced in narrow arcs, the female sometimes stepped toward him and then either fled suddenly or remained inactive. When a female remained inactive, a male that got close either brought his legs I over her and began to mount, or else he backed away from the quiescent female.

While only about 40 mm away from the female, it was common for males to switch suddenly from hunched posturing and swaying to zigzag dancing. Linear dancing and spurting were typically interjected briefly and intermittently during a sequence of zigzag dancing, erect posturing and hunched posturing. When linear dancing, a male stepped forward and backward several times with or without first pausing and with amplitude (distance moved forward or backward) rarely exceeding 50 mm (about 20 mm was typical). When spurting forward, the male usually lowered his erect legs I, placed his tarsi on the ground while stepping forward, and then moved legs I back to the erect posture (position 3), when he stopped.

How propulsive displays, fleeing and chasing were integrated into sequences

Propulsive displays, being interjected suddenly and seemingly unpredictably, were routine in male-female, male-male and female-female interactions, and they were combined in highly variable ways with other behaviour patterns. Immediately after one spider performed a propulsive display in a same-sex interaction, the other spider or both spiders usually turned and fled. For example, when one spider made a long leap and contacted another spider, the contacted spider sometimes landed on its back and then, after 1–30 s, regained its footing and fled while the other spider watched. However, except for charging (see below), fleeing did not so routinely follow propulsive displays during male-female interactions.

Sometimes a male approached a quiescent female by zigzag dancing and then suddenly made a truncated leap towards her, after which the male usually resumed zigzag dancing, or less often he hunch postured and swayed while the female watched, but leaping was more often performed by females. It was common for a female to make a single long leap or to make several truncated leaps in rapid succession toward a male. Males that were posturing when the female leapt tended to hold their ground and continue posturing, and males that were not already posturing often began posturing when leapt at. If a female stopped immediately in front of a male after leaping, it was common for the male to extend his legs over her in erect position 1 or 2, sometimes with mounting and mating following soon afterwards.

Sometimes females repeatedly charged toward males, with the interval between successive charges being only a fraction of a second (each charge in bout moving her forward only about 10 mm). If the male was dancing when the female charged, he often

fled, with the female chasing after him. Then, when the female stopped chasing, the male usually turned around and displayed by posturing with legs erect or hunched.

When a female fled, the male often chased after her, and sometimes he zigzag-danced or maintained erect posturing (especially position 3) at the same time while chasing her. Males sometimes made successive long leaps at a fleeing female, and occasionally the leaping male contacted the female briefly one or more times from the rear.

How arched, erect and hunched posturing was integrated into sequences

Hunched posturing was adopted by males and by females, in same-sex and in male-female interactions, but there were differences in how hunched posturing was used by the two sexes. For example, when females hunch postured, they usually kept their palps in the normal posture, and their palps were not especially active. Males, however, often waved and stepped with their palps while hunched posturing. When inactive, the male's palps were usually retracted or arched.

Males sometimes, but females only rarely, adopted a routine of repeatedly taking a few steps with legs held in the normal posture and then standing for several seconds with legs hunched or erect (especially in position 3), with there being no obvious rule pertaining to whether hunched or erect posturing was adopted when the spider stopped.

Hunched posturing was common in male-male interactions, but the two males often postured in different ways (e.g., one male posturing for a long time with one leg I hunched and with other leg I erect in position 3, while the other male was posturing with both legs I hunched).

Arched and erect posturing were frequently adopted during same-sex and male-female interactions. During male-female interactions, males especially often erect postured in position 3. While facing an arched- or erect-posturing male, it was common for a female to flick intermittently while posturing with arched or erect legs, or to wag while posturing with hunched legs. However, it was common for both sexes in all types of interaction to switch frequently between arched, hunched and raised posturing.

In longer interactions, posturing males sometimes froze when females became quiescent or quiet. On rare occasions, males sustained the frozen posture for many minutes at a time, or even for an hour or more, but 10–60 s was more typical. Although males froze with legs arched or hunched, it was more ommon for them to freeze with legs raised (especially erect position 3). On rare occasions, a male switched from a frozen posture to being active while the female was still more or less quiescent, but freezing more often ended when the female began walking away. When a male broke out of freezing, even if the female was still quiescent, he often immediately began dancing towards her.

In the course of an interaction, a male sometimes ended up at the top of a cage with the female below. In these instances, the male sometimes attached a silk line to the top of the cage and then, holding on to this line, dropped down toward the female, sometimes erect posturing while suspended on the silk line.

How swaying and wagging were integrated into sequences

Repeated alternation between hunched posturing and swaying (hunch-sway alternation) was characteristic of females and of males in male-female and in same-sex interactions. However, it tended to be only one individual that adopted hunch-sway alternation in any one sequence, the other individual more often hunched posturing without swaying.

When males alternated between hunched posturing and swaying while interacting with females, there was usually a corresponding alternation in male palp activity: stepping with palps while hunched posturing and holding palps stationary in the low retracted posture while swaying. Males often leapt at females immediately after a bout of hunch-sway alternation. When the male leapt toward her, the female sometimes leapt away and fled immediately, with the male often running and leaping after her. There were rare occasions, however, when a female stood her ground after a male leapt at her, even when the leaping male contacted her.

There were two primary situations in which males swayed during male-male interactions: (1) The two males faced each other and swayed at the same time, with it being usual for each male to sway at the same time to his own right side and then for each male to sway at the same time to his own left side; (2) One male held legs hunched while stepping to the side and then swayed as soon as he stopped stepping, with these step-stop-sway sequences sometimes being performed by both males at the same time.

Males often, but females only rarely, wagged intermittently while posturing with their legs hunched, with the timing of wagging appearing to be unpredictable. In male-male interactions, it was common for hunched posturing and wagging to

follow rapidly after a bout of erect posturing. For example, sometimes one male suddenly switched from erect to hunched posturing, followed by the other male wagging and backing away with legs hunched.

How abdomen twitching was integrated into sequences

Abdomen twitching was a routine part of the male's pre- and post-contact behaviour during male-female interactions at and away from nests. For example, males twitched their abdomens almost continuously when mounting females and when they had their palps engaged, with higher-amplitude and especially forceful abdomen twitching being common during palp switchover. Males often twitched their abdomens when erect or hunched posturing, with each individual bout of abdomen twitching lasting for several seconds at a time and with numerous bouts typically following one after the other.

Males routinely twitched their abdomens while probing or chewing on nests. Males that were on or near a female's nest twitched their abdomens sometimes while just walking or standing. At or near a nest, abdomen twitching was usually performed intermittently for a few seconds at a time, but there were rare occasions when males twitched their abdomens continually for sustained periods lasting as long as many minutes at a time.

Females twitched their abdomens during male-female interactions, but not so noticeably or frequently as males. Individual bouts of abdomen twitching by females usually lasted c. 0.5 s, although there were rare occasions when females twitched their abdomens for several seconds, or even minutes, at a time.

Females only rarely twitched their abdomens during interactions with other females, but abdomen twitching was routine in male-male interactions.

Male-male interactions away from nests

When two males were approaching each other, it was usual for one or both to posture with legs hunched or arched, and frequently one or both wagged. Intermittently and seemingly unpredictably, one or the other male wagged, flicked, swayed, rocked, waved palps side to side or performed propulsive displays. Males sometimes embraced during longer interactions. While embracing, fangs were extended, and it was also common for males to hold their fangs extended even when not in contact, with the magnitude of fang extension being highly variable. Retracted was the most common palp posture.

Female-female interactions away from nests

One or both females typically postured, especially in erect position 3, with cephalothoraxes raised and with palps either arched in or held in the normal palp posture. One or both females usually switched repeatedly between posturing with legs erect and adopting the prey-stalking posture while slowly approaching the other female. Whenever a female came to within about 10 mm of the other female, one or both usually fled. When only one female fled, the other only rarely followed.

Female-female and male-male interactions at nests

When the resident was quiescent inside a nest, the intruder usually began by probing and then, after pushing its face energetically into the silk, chewed and tugged. The resident spider often responded by pulling on the silk.

Sometimes during male-male interactions, there were brief bouts of the intruder palpating or probing, or both, on the nest silk, with accompanying intermittent abdomen twitching. At nest doors, two males (sometimes) or two females (rarely) embraced, lunged or both.

Male-female interactions away from nests

Regardless of whether the male-female pair mated, male-female interactions away from nests were complex, highly variable and hard to characterise. Males in particular appeared to run through much of their large repertoire of display behaviour in endlessly varying arrangements. Female behaviour may have been less variable, but no particular female behaviour pattern provided a clear-cut prediction of whether or not the female would subsequently mate.

Although there were rare instances of females head-standing in female-female interactions, this uniquely female behaviour was performed primarily in male-female interactions. Females usually performed a head-stand for a few seconds and then immediately fled, but there were rare instances of females performing head-stands for several minutes at a time before fleeing.

Females often performed head-stands, propulsive displays, erect posturing or hunch posturing and then mated, with mating sometimes coming almost immediately after the performance of one of these seemingly aggressive behaviour patterns. At the other extreme, females sometimes appeared passive for most of the interaction and even allowed males to mount, and then fled and failed to mate.

It was common for a female to make lunges or truncated leaps when a male was only a few millimetres in front of her, including when a male was quivering with his legs over her, after which she might or might not mate. Sometimes females leapt over erect-posturing or dancing males, or else leapt almost straight up, and then fled, after which they might or might not mate later in the interaction.

Embracing may have been the closest thing to behaviour predicting female rejection of a male (i.e., pairs that embraced only rarely mated), but embracing was not a routine preliminary to females rejecting males (i.e., embracing was rare during all male-female interactions, regardless of whether mating did or did not follow).

Male-female interactions at nests

Unlike other salticids studied (Jackson & Pollard 1997), the distinction between at-nest and away-from-nest male-female interactions was typically blurred in *E. culicivora*. This was because females often left and then re-entered their nests during the interaction, because females often stood with their front legs and the front ends of their bodies extending out of a nest door and males often displayed from a distance at these exposed females. Even when resident females seemed not to be visible to the male and even when the female was absent from the nest, males that were oriented in the direction of a nest often adopted displays typical of male-female interactions away from nests (i.e., males often seemed to be directing posturing and dancing at the nest itself rather than at a female).

Once a male arrived at a nest's door, he usually began probing immediately. If the male arrived on the nest away from the door, sometimes he probed away from the door, but more often he moved to the door before beginning to probe. Females usually held the door down while the male probed.

Sometimes males and females went back and forth between doors (i.e., the male moved away from the door at which the female was pulling on silk, walked over the nest to the opposite door and began to probe there, with the female usually moving quickly through the inside of nest to this door and pulling on it). There were also rare instances of the female leaving the door at which the male was probing and going through the inside of the nest to the opposite door. When this happened, the male usually did not enter but instead walked across the nest to the door at which the female was now located and resumed probing.

Periods during which a male and female were highly active sometimes alternated with quiescent or quiet periods that sometimes lasted 5–10 min, but on rare occasions lasted several hours.

Males usually alternated at highly variable intervals between being at the nest and being away from the nest. Periods away from nests usually lasted only a few seconds or minutes, although there were rare instances of staying away for up to an hour. While away, the male sometimes stepped about actively in a localised area beside and near the nest, generally moving no more than 10 mm from the nest and facing the nest for most of the time while away. There were intermittent bouts of chewing by the male, but the location of chewing followed no discernible pattern. Between chewing bouts, the male sometimes stood for several seconds or minutes at a time with his face pressed against the silk.

It was usual for males eventually to begin probing with legs I extended through a door and to ease themselves through the nest door in successive 0.5 s bouts. Sometimes the probing male moved his legs to erect position 1 or 2, and sometimes he also held his palps erect or semi-erect. As the male entered the nest, he often tapped and probed with his palps and, once he had his body at least partly in the nest, he advanced toward the female, sometimes with intervening periods of the male and female being quiescent, with the male holding his legs extended over the female in erect position 1 or 2.

Cohabitation

There were about 50 observations of males cohabiting with subadult females in the field, either with each spider in a separate chamber of a dual nest (two silk tubes woven together, with the doors of one chamber aligned with the doors of the other chamber) or, more often, with the male standing on or near the female's nest but not in a silk chamber.

In the laboratory, when a male encountered a subadult female in a nest, the two spiders interacted in much the same way as in male-female interactions, but without the male mounting the female. Sometimes a female left her nest while a male was still outside or else the male entered a nest, with the female inside, followed soon afterwards by the male and the female both leaving the nest. When a female left her nest, the male usually remained near or in the nest. Sometimes she left the nest's vicinity and the interaction ended, but there were other times when the female remained nearby for several minutes or hours and then returned and entered the nest again.

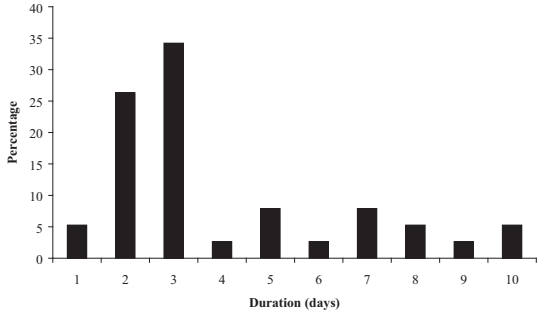


Fig. 29 Cohabitation duration. How long *Evarcha culicivora* male remained with subadult female before she matured and the pair mated (mean ± SD = 4.00 ± 2.51, $N = 38$).

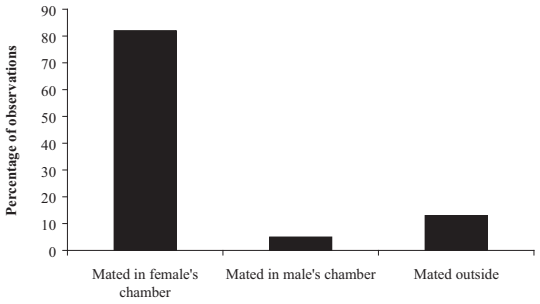


Fig. 30 Location of mating by *Evarcha culicivora* after cohabitation ($N = 38$).

If the male was in the nest when she returned, he usually left the nest several seconds or minutes later and then remained in the vicinity.

Successful cohabitation (i.e., instances that ended with the female moulting and the pair mating) lasted 1–10 days (Fig. 29). Most males gradually spent more and more time spinning silk on and near the subadult female's nest, usually completing an enclosing chamber within 1–2 days. After the female matured, the male most often mated with the female inside her chamber, although there were instances of the female first coming out of her chamber and the pair mating outside or in the male's chamber (Fig. 30).

Mounting and post-mount pre-copulatory behaviour

Regardless of whether the female was in her nest or out in the open, there were similar and predictable sequences immediately preceding copulation. Just before mounting, the male and female were usually facing and usually the male had his legs extended in erect position 1 or 2 over the female's carapace. Often the male's palps were in forward erect position 1, sometimes with tarsus tips touching the female's face.

Although the male typically tapped the female with his legs I and then quivered his legs I over her, there were also rare bouts that lasted c. 0.5 s during which males tapped and quivered at the same time, quivered only or tapped only. Sometimes a female repeatedly jerked back or else stepped a few millimetres away (backwards or to the side), stopped, and then let the male move forward and quiver again. Alternatively, the female turned and walked away, only to turn and face the male again, sometimes posturing (typically in erect position 3) at a male and then allowing him to resume quivering.

Sometimes a male succeeded in mounting by stepping over a female's hunched or raised legs, and raised cephalothorax. After lowering her legs and body, the female sometimes mated with the male. There were rare instances of a male zigzag dancing and, when close, moving his erect legs I (position 1 or 2) over a female that was facing 45–180° away. When this happened, the male sometimes mounted the female while she continued to face away from him. However, successful mounting usually began with the female facing the male, her body lowered (Fig. 9 and 25) or in the rest posture, and her legs raised (position 3) or hunched.

Copulation

During copulation, defined by palp engagement (palpal organ of one palp positioned against one side of female's epigynum), *E. culicivora* adopted the copulatory posture (Fig. 6) that is typical of most salticids (male dorsal to the female; male and female facing opposite directions: Posture 2 in the classification of Gerhardt & Kaestner 1938; see Jackson & Pollard 1997). The male's haematodocha (membranous part of the palpal organ) pulsated intermittently during palp engagement (Fig. 6).

There was no clear preference for the male to engage his left or right palp first: left palp first: $N = 22$; right palp first $N = 16$; test for goodness of fit, $\chi^2 = 0.947$, $P = 0.330$). About 2 min later, he switched to the other palp (Fig. 31). About 2 min later, the male switched palps again. If the female remained more or less quiescent, the male usually continued

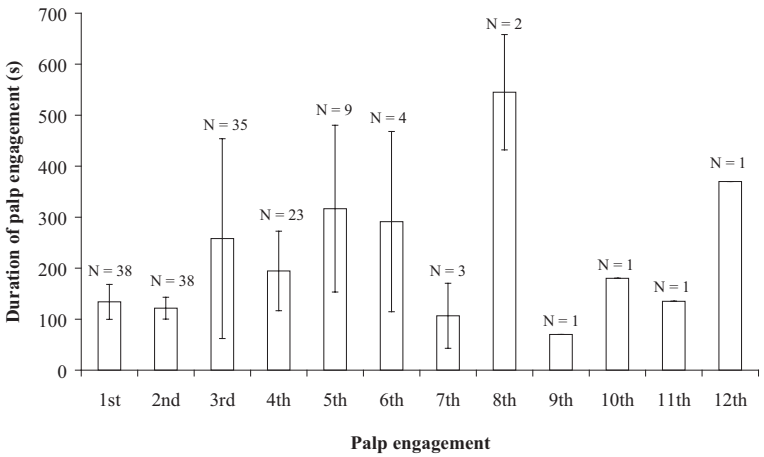


Fig. 31 Duration (mean ± SD) of each successive palp engagement.

to alternate palps (Fig. 32), but successive palp-engagement duration now became more variable. Sequencing also became more variable (i.e., there was occasional re-engagement of the same palp instead of strict alternation).

During the interval between palp engagements, the female's abdomen regained alignment with the cephalothorax and the male usually moved back to the centre of the female's abdomen. The male's haematodocha, which was often still inflated immediately after he disengaged his palps, was usually deflated by the time the male was centred over the female. Centred over the female, the male resumed rubbing and tapping. If the female remained more or less quiescent, the male soon resumed copulation, but eventually he walked away from the female and the interaction ended.

Between or during palp-engagement intervals, females sometimes raised legs I, began walking or both. Males were typically dislodged when females began walking, but the dislodged male often displayed, mounted and renewed copulation. There were rare instances of a female walking for a few seconds or even several minutes, with the male remaining mounted. He continued to rub and tap and eventually he sometimes resumed copulation.

Kicking

Males always kicked, either intermittently or continuously, when their palps were engaged, and sometimes they kicked after mounting but before the initial palp engagement or between successive palp engagements. On rare occasions, males kicked while moving over a female, but before fully mounted.

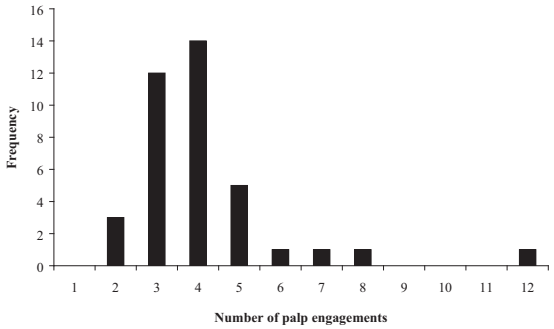


Fig. 32 Total number of palp engagements per copulation (mean ± SD = 4.11 ± 1.81, $N = 38$).

When an individual palp engagement lasted for 60 s or longer (i.e., during most palp engagements), it was common for a male to adopt a routine of twitching his abdomen and kicking at the same time, his abdomen moving down simultaneous with his legs moving down. After legs IV reached the lowest position in the kicking cycle, the male then continued twitching his abdomen for c. 1 s longer.

When a female became active while a male was kicking, the male usually began kicking faster and more forcefully. When a female became active while a male was not kicking, although he had his palp engaged, he almost always started kicking immediately.

Fig. 33 *Evarcha culicivora* male (above) preying on female (below) immediately after courtship. Male's chelicerae gripping female's posterior carapace (both spiders facing to left). Immediately beforehand, female turned and fled from displaying male, whereupon male chased, leapt and killed female.

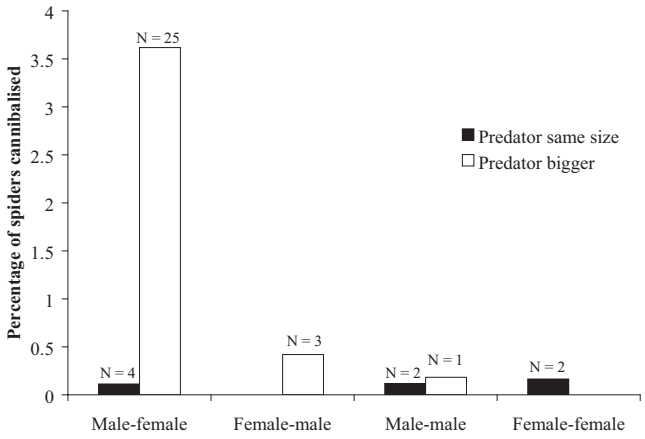


Fig. 34 Percentage of *Evarcha culicivora* interactions that ended with cannibalism: one spider ("predator") killed other ("prey"). Male-female: male was the predator. Female-male: female was the predator. There were no instances of smaller spider killing larger spider.

Cannibalism

Cannibalism (i.e., one individual killing and eating another during intraspecific encounters) was observed primarily when the two individuals differed in body length, with the larger of the two individuals usually being the predator. For instance, of a total of 3335 same-size male-female encounters, four males killed females, whereas 3331 males did not kill females. In 691 different-size male-female encounters (male larger), 25 males killed females, whereas 666 males did not kill females (test of independence, $\chi^2 = 97.94$, $P < 0.001$). Most instances of cannibalism were during male-female away-from-nest encounters during which there was no interaction (i.e., the predatory individual stalked and attacked the other individual seemingly before the prey individual became aware of being stalked).

It was more common for males to kill and eat females than vice versa (Fig. 33 and 34). The typical preliminary to cannibalism during male-female interactions was for one spider to flee and the other spider to leap on and kill it. However, there were also instances of males displaying at a quiescent female, continuing to display while approaching and then killing her when he got close, typically switching suddenly from displaying to attacking. There were also instances of males mounting and initiating postmount courtship, and then killing the female on which he was mounted while she was quiescent, with or without her abdomen being rotated.

Fig. 35 Male-female pair of *Evarcha culicivora* interacting on *Ricinus communis*. Female partly obscured by vegetation (below).

Fig. 36 *Evarcha culicivora* male (above) standing on *Lantana camara* flower and pre-mount tapping female that is standing below on leaf (facing away in photograph). Female's dorsal carapace faces male. Male viewed side on (his dorsal body turned to left in photograph). Male's legs I contacting left side of female's cephalothorax.

While copulating with a quiescent female, there were instances of the male suddenly biting and killing the female, after which one of four possible actions followed: he ate the female immediately, walked away without eating her, attempted to continue copulating and then ate her or attempted to continue copulating and then walked away without eating her.

Interactions on *Lantana camara* and *Ricinus communis*

All the behaviour categories seen during interactions in bare cages were also seen during interactions on *L. camara* and *R. communis*, and vice versa. Sequences during interactions when on *L. camara* and *R. communis* were also in basic respects similar to interactions when the spiders were in bare cages. However, interactions on *L. camara* and *R. communis*, especially male-female interactions, were distinctive because of much greater variability in the performance of individual categories of behaviour and in sequencing.

With the two spiders moving about actively through the dense inflorescences (especially on *L. camara*), each spider's view of, and path to, the other spider was routinely occluded by the flowers and other vegetation (Fig. 35). It was common for one spider to leap about on the plant, with the other spider usually orienting toward the leaping spider and this spider's orienting response, in turn, attracting the attention of the spider that had been leaping. Another impression we got from observation was that sometimes, when a male saw a female before she saw him, he deliberately hid behind leaves and stems, or in the inflorescence, until the female passed by, and then he suddenly emerged and began posturing (Fig. 21A) or dancing.

In bare cages, when one spider departed or fled from the other spider, this was primarily by walking or running, but spiders on plants often shuffled or dodged out of the way by quickly moving under vegetation, leaping from one part of the plant to another or dropping on a dragline to a lower part of the plant. There were also instances of one spider dropping on a dragline from higher up in the vegetation toward another spider lower down, with males approaching females this way more often than vice versa and sometimes posturing as they did so.

It was routine for one spider to display at another spider that was facing up, down, left, right or at almost any conceivable angle (Fig. 36), with the displaying spider often tilting so as to achieve closer

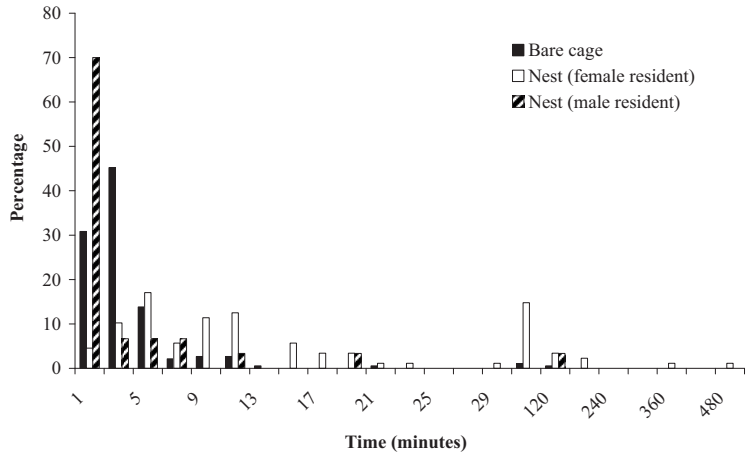


Fig. 37 Duration (min) of male-female interactions, with or without nests present (bare cage: mean ± SD = 4.81 ± 14.35, *N* = 188; nest (female resident): mean ± SD = 33.50 ± 69.79, *N* = 88; nest (male resident): mean ± SD = 6.70 ± 21.75, *N* = 30).

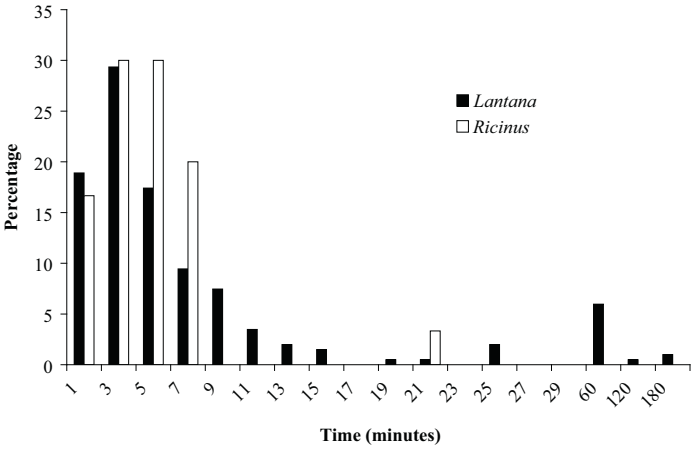


Fig. 38 Duration (min) of male-female interactions on *Lantana camara* and *Ricinus communis* (*Lantana*: mean ± SD = 10.81 ± 23.24, *N* = 201; *Ricinus*: mean ± SD = 4.67 ± 3.68, *N* = 30).

approximation to being head-on and oriented in the same plane with the other spider.

Dancing was especially complex on plants. While moving in an arc during a zigzag dance, for example, a male sometimes had to maintain his footing on a slender shred of vegetation, make repeated leaps from flower to flower, and so forth. The male's dancing path sometimes took him one or more times from the top side to the bottom side of a leaf and back, or vice versa. Although combining zigzag dancing with linear dancing was uncommon when in bare cages, males often combined zigzag dancing with linear dancing when on plants. For example, males sometimes linear danced by moving up and down the stalk of a plant after zigzag dancing on a flower or leaf.

When in the vegetation, mounting and mating often appeared to be especially challenging. Sometimes the male began pre-mount tapping while reaching from a part of the vegetation where he was standing to another part where the female was standing (Fig. 36), with mounting being achieved not by simply walking forward over the female, as was routine in bare cages, but instead by moving over the female from some other angle. When the female was buried deep within an inflorescence, it often seemed impossible for males to mount, yet males tried and sometimes succeeded in reaching over to the female's rotated abdomen to engage a palp, sometimes with a leaf or a stem running between the male and female.

Interaction durations

The data we review here were durations recorded from a representative subset of each interaction type.

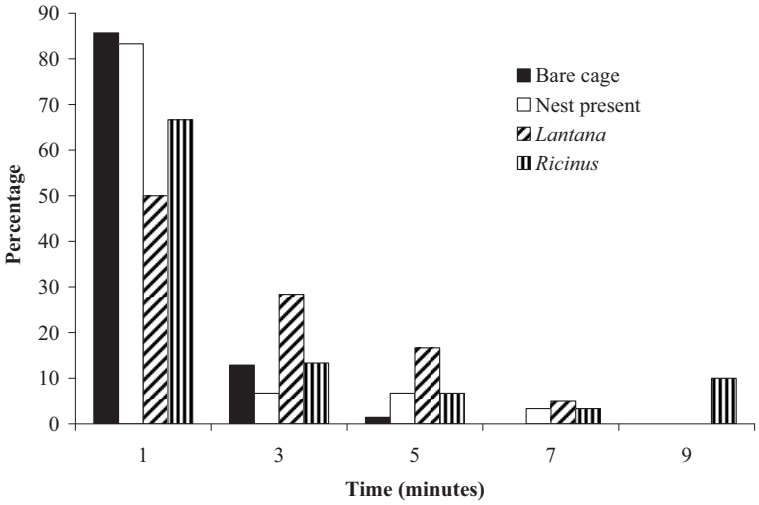


Fig. 39 Duration (min) of male-male interactions (bare cage: mean ± SD = 1.55 ± 1.49, N = 80; nest present: mean ± SD = 1.40 ± 1.22, N = 30; *Lantana*: mean ± SD = 3.77 ± 3.08, N = 60; *Ricinus*: mean ± SD = 4.60 ± 2.94, N = 30).

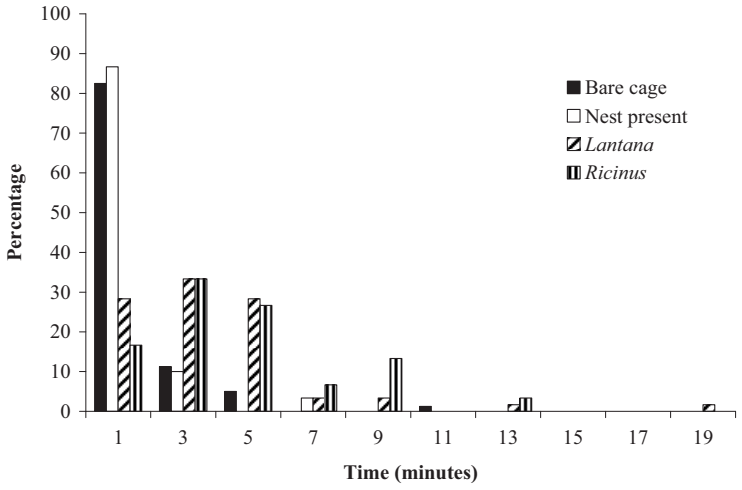


Fig. 40 Duration (min) of female-female interactions (bare cage: mean ± SD = 1.31 ± 0.81, N = 70; nest present: mean ±SD = 1.60 ± 1.50, N = 30; *Lantana*: mean ± SD = 2.53 +/–1.82, N = 60; *Ricinus*: mean ± SD = 2.53 ± 2.66, N = 30).

When in bare cages with no nests present, some male-female interactions lasted for hours, although 2–5 min was more typical (Fig. 37). Interactions when males encountered females in nests usually lasted 10–60 min, although they sometimes lasted for many hours and, in rare instances (not part of our recorded samples), several days. Male-female interactions at nests were significantly longer than male-female interactions in bare cages (male resident at nest: Z = 2.51, P = 0.012; female resident: Z = 9.70, P < 0.001; Mann-Whitney U-tests). Interactions at nests where the female was the resident were significantly longer than interactions at nests where the male was the resident (Z = 5.96, P < 0.001).

As durations of male-female interactions on *Lantana camara* were not significantly different from durations of male-female interactions on *Ricinus communis* (Z = 0.74, P = 0.46; Fig. 38), we pooled these data ("on plants"). Male-female interactions were significantly longer on plants than in bare cages (Z = 8.73, P < 0.001).

Males displayed actively when interacting with each other, but usually only briefly (1–5 min being typical) (Fig. 39). Female-female interactions were also short, usually lasting 1–5 min (Fig. 40). Male-male and female-female interactions at nests were not significantly longer than interactions in bare cages (males: Z = 0.35, P = 0.73; females: Z = 0.29,

$P = 0.78$). For male-male and for female-female interactions, durations on *Lantana camara* were not significantly different from durations on *Ricinus communis* (males: $Z = 1.48$, $P = 0.139$; females: $Z = 0.89$, $P = 0.38$), and we pooled these data ("on plants"). Using the pooled data, male-male and female-female interactions were significantly longer on plants than in bare cages (males: $Z = 6.86$, $P < 0.001$; females: $Z = 3.54$, $P < 0.001$).

In bare cages, male-female interactions were significantly longer than male-male interactions ($Z = 6.71$, $P < 0.001$) and female-female interactions ($Z = 7.09$, $P < 0.001$), but durations of male-male interactions were not significantly different from durations of female-female interactions in bare cages ($Z = 0.41$, $P = 0.68$). On plants, male-female interactions were significantly longer than male-male interactions ($Z = 2.51$, $P = 0.012$) and female-female interactions ($Z = 6.53$, $P < 0.001$), and male-male interactions were significantly longer than female-female interactions ($Z = 3.95$, $P < 0.001$).

DISCUSSION

Although the display behaviour of *E. culicivora*, on the whole, fits within the prevalent pattern known from recent research on other salticids, there are also some interesting differences.

Crane's (1949) conclusion that visual stimuli are both necessary and sufficient for releasing salticid courtship (defined as intersexual communicatory behaviour that forms the normal preliminaries to mating; see Jackson 1982a) may have been compatible with commonsense expectations about adaptive tradeoffs in small animals, yet there are now numerous studies illustrating that salticids make extensive use of acoustic, percussion (seismic), silk-borne, tactile and chemical signalling during intraspecific interactions (Edwards 1981; Gwynne & Dadour 1985; Jackson 1987; Pollard et al. 1987; Maddison & Stratton 1988; Noordam 2002; Elias et al. 2003, 2005).

Courtship versatility is an especially striking example of how salticids make extensive use of other sensory modalities despite their exceptional eyesight. First documented in detail in a study of a North American species, *Phidippus johnsoni* Peckham & Peckham (Jackson 1977), "courtship versatility" refers to a conditional strategy of male salticids where they use vision-based displays when they encounter mature females outside nests (type 1 courtship), use silk-borne signals when they encounter adult females inside nests (type 2 courtship), and cohabit with subadult females (i.e., make a second chamber fastened to subadult females' nests where they wait until the subadult female matures; see Jackson 1986). Vision is necessary and sufficient for eliciting the type 1 courtship of many, but not all (see Elias et al. 2005), salticids. However, salticids readily communicate with type 2 courtship in total darkness (Jackson & Pollard 1997). We documented courtship versatility for *E. culicivora* and this conditional strategy may, in fact, be a universal characteristic of salticid spiders, as every detailed published study designed to look for evidence of this conditional strategy has succeeded in documenting it (for references, see Jackson 1992; Jackson & Pollard 1997). Post-contact tactile or chemotactic courtship, a phase common to type 1 and 2 courtship, was also documented for *E. culicivora* and may also be universal in salticid courtship.

Another characteristic of *E. culicivora* is the adoption of a repertoire of distinct display elements during type 1 and during type 2 courtship, with the way elements are combined and sequenced being highly variable. This also may be universal for salticids (Jackson & Pollard 1997). Although the influence of classical ethology (for references see Tinbergen 1963) was evident in how much of the early literature characterised salticid display behaviour as stereotypic and reflex-like (Heil 1936; Crane 1949; Drees 1952), later work has largely supplanted this portrayal with an emphasis on how salticid intraspecific interactions tend to be highly variable and complex (Jackson & Pollard 1997; Elias et al. 2003).

It is likely that the evolution of salticid display complexity has been driven by sexual selection (Jackson & Pollard 1997). Sexual selection has, in fact, been a dominant topic in the literature on salticid courtship from the 19th century to the present (Peckham & Peckham 1889; Bristowe 1941; Jackson 1981; Richman 1982; Masta & Maddison 2002; Hebets & Maddison 2005; Elias et al. 2006), and hypotheses concerning sexual selection in salticids have most often pertained specifically to intersexual selection (i.e., selection resulting from mate choice; see Harvey & Bradbury 1991). Consistent with the prevailing trend in the animal kingdom as a whole (Bradbury & Anderson 1987), in salticids males typically display more persistently than females during male-female interactions (Jackson & Pollard 1997), with females tending to alternate between watching the male and moving a short distance away. Salticid females are typically envisaged as determining

whether mating takes place (i.e., it is primarily the female that does the choosing) by either allowing or not allowing the male to approach, mount and copulate.

Female choosiness seems to account for male behaviour relatively easily (i.e., the male's mating success depends on doing what the female prefers), but precisely what advantage females might gain by favouring particular types of male courtship remains uncertain for *E. culicivora*, as it does for salticids in general (see Jackson & Pollard 1997; Hebets & Maddison 2005; Elias et al. 2006). Yet, with *E. culicivora*, and perhaps with numerous other salticids (see Hoefler 2007), the traditional way of phrasing this question about sexual selection needs to be revised. *Evarcha culicivora* appears unconventional because both the male and the female of this species display actively and both sexes are prone to initiating courtship. From other studies, we have evidence that both sexes of *E. culicivora* exercise pronounced mate-choice behaviour, choosing on the basis of the body size of potential mates (Cross et al. 2007) and also on the basis of the odour potential mates acquire by feeding on blood-carrying mosquitoes (Cross & Jackson unpubl. data).

Sexual cannibalism is another topic that has a long history in the literature on spider courtship, and *E. culicivora* seems to go against tradition here as well. Female spiders, according to conventional wisdom, are ravenous predators and males need to identify themselves or else risk being perceived as prey (Robinson 1982). Certainly there are spider species for which conventional sexual cannibalism (i.e., females eating males) is frequent during courtship and mating (Elgar 1992; Schneider & Lubin 1998; Andrade 2003) and, regardless of whether it is frequent or not, the potential of cannibalism seems to be generally applicable for courting spiders, as all spiders are predators of other arthropods, including arthropods that are similar in size to a potential mate. However, for salticids (Jackson 1982b; Richman & Jackson 1992; Jackson & Pollard 1997), and perhaps for spiders in general (Jackson & Pollard 1982, 1990), the idea that males reduce their risk of being eaten by identifying themselves to females as non-prey does not hold up well to close scrutiny.

Envisaging identification as being primarily the female's problem is a peculiar bias in the literature on the cannibalism-identification hypothesis, because it seems to overlook the fact that salticid males do not normally display indiscriminately. On the contrary, they tend to reserve courtship displays specifically for encounters with conspecific females. By displaying first, a male demonstrates that he has identified a female without needing to see her display. Moreover, males are primed to escalate conflict more intensely during encounters with other conspecific males when they can see that a conspecific female rather than some other organism, such as a heterospecific female or a prey item, is present (Wells 1988; Cross et al. 2006; Jackson et al. 2006). Given that males can accurately identify females without females necessarily displaying at them, an explanation would be needed if females were shown to not have comparable perceptual ability. *E. culicivora* is one species for which it is clear that females certainly do have this ability, as females of this species frequently displayed first.

Another problem with the cannibalism-identification hypothesis is that, although cannibalism may be a significant risk during encounters between conspecifics, this risk runs both directions. In the Salticidae (Jackson 1982a, 1992) and other spiders (Jackson & Pollard 1990), we see males eating females as well as females eating males, along with males eating other males and females eating other females. For salticids, with their extraordinarily good eyesight, misidentification seems to have little to do with who eats whom. *E. culicivora*, in particular, seems to turn the traditional identification-cannibalism hypothesis on its head because, during courtship and mating, males of this species are apparently more dangerous to females than females are to males.

When we consider *E. culicivora*, it might be tempting to flip the cannibalism-identification hypothesis around and argue that the unusually active way females display at males is an adaptation by which females identify themselves as non-prey to males, but this is a superficial explanation for display complexity in this or any salticid species. For understanding the ultimate causation of salticid display complexity, simplistic emphasis on identification can be counted on to be misleading. As has been suggested elsewhere (Jackson & Pollard 1997), a more realistic perspective might be derived from ideas related to sensory exploitation (e.g., Proctor 1992; Clark & Uetz 1992, 1993; Ryan et al. 2001) and receiver psychology (e.g., Guilford & Dawkins 1991; Rowe 1999), but with greater emphasis on complexity, flexibility and dynamic interaction between signaller and receiver. This may seem like a subtle distinction, but this is a significant departure from the idea that the male's problem (and, for *E. culicivora*, the female's problem as well) is simply to use an identification signal as a way to turn off the predatory inclinations of a potential mate. For the

male and for the female salticid, courtship just does not appear to be fundamentally about a displaying individual revealing that, rather than being just another potential meal, he or she is a potential mate.

It may often be more useful to envisage each displaying salticid as orchestrating a careful balance between stimuli that provoke and stimuli that inhibit predatory attacks from the other salticid, as though the male and the female were each playing mind games with a predator, something similar to a lion trainer and a lion, where each salticid is analogous to the trainer and to the lion at the same time (Jackson & Pollard 1997). Simple identification would be more compatible with highly stereotypical courtship, not the complex, highly variable sequences actually found in salticids. With *E. culicivora*, a species with especially variable, complex display behaviour, we may have found a species that is especially appropriate for future research that examines the mind-games hypothesis more carefully.

Lesser variability may be characteristic of the display behaviour of some other salticids. For example, the females of some salticid species (e.g., *Maevia inclemens*) are said to perform receptivity displays (Clark & Uetz 1993; Clark & Biesiadecki 2002) (i.e., displays after which mating is almost certain not to be resisted by the female). However, in the display repertoire of *E. culicivora*, and that of all salticid species investigated in the University of Canterbury Spider Laboratory (Jackson & Pollard 1997), no comparable receptivity signals have ever been evident.

Selective attention is an often neglected topic in the mate-choice literature (see Dukas 2002), but much of *E. culicivora*'s display behaviour may function in attracting the attention, and sustaining the attention, of potential mates. Interaction complexity, and especially the adoption of displays that are rich in movement, may function in part as anti-habituation mechanisms (Jackson 1982b). Resurrecting long-forgotten, yet still important, ideas from the literature on bird song, *E. culicivora*'s display behaviour might be explained in part as each individual striving to avoid the other individual's "monotony threshold" (see Hartshorne 1956, 1958).

The variability of *E. culicivora*'s display behaviour may be especially relevant when considered in the context of courting and mating in the dense inflorescences of plants, especially *L. camara* and *R. communis*, where the surfaces on which the interacting spiders move about is complex and visual obstructions intervene between the spiders as they exchange signals. *E. culicivora*'s display behaviour often appeared more exaggerated when individuals met on plants, and perhaps being predisposed to meet on the foliage of plants functions as a means by which spiders challenge each other's ability to orchestrate complex display behaviour. Setting up challenges of this sort might function in the context of intersexual selection (see Andersson 1994).

The mating behaviour of *E. culicivora* also appears to be unusual in comparison to other salticids, forcing us to reconsider the definition of courtship as intersexual communicatory behaviour that forms the normal preliminaries to mating (Jackson 1982a). There has been considerable recent interest in potential examples of copulatory courtship in animals (i.e., communicatory behaviour during, instead of strictly before, mating; see Eberhard 1991, 1994; Edvardsson & Arnqvist 2000), and a long-standing interest in this topic in the Salticidae in particular (see Jackson 1980). The kicking behaviour of *E. culicivora* males is normally performed while mating and this behaviour pattern, which is unique for salticids studied to date, may be an especially rewarding example of copulatory courtship for future research. One of the hypotheses that should be considered is that females make decisions about whether to use a male's sperm on the basis of his kicking behaviour during copulation (see Hoikkala et al. 2000). Kicking may also be a way in which males avoid exceeding the female's monotony threshold, as suggested by the male's variable kicking rhythms and by how variability seemed to increase when previously quiescent females began moving.

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